Zinc Uptake by Hyparrhenia rufa (Nees) Stapf and
Indigofera hirsuta L. in Selected Eastern Panamanian Soils

By

MICHAEL WILLIAM SILVEY

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Dedicated to my father,

the late William John Silvey

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Graduate Council of the University of Florida in Partial Fulfillment
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ZINC UPTAKE BY HYPARRHENIA RUFA (NEES) STAPF AND
INDIGOFERA HIRSUTA L. IN SELECTED EASTERN PANAMANIAN SOILS

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Michael William Silvey

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This study was conducted as part of the Bioenvironmental and
Radiological-Safety Feasibility Program for the proposed nuclear ex-
cavation of an Atlantic-Pacific interoceanic sea-level canal. Zinc
was selected for uptake studies by jaraguagrass (Hyparrhenia rufa
(Nees) Stapf) and hairy indigo (Indigofera hirsuta L.) in eastern
Panama because of the relatively sparse knowledge of its behavior in
tropical soils and forage crops.

The primary objectives were to gain insight on (a) the interrela-
tionship of zinc with other macro- and micronutrients in the forage
plant and soil, (b) the factors regulating the availability of zinc in
the soil and its assimilation by forage plants, and (c) possible radio-
zinc uptake and measures for reducing forage uptake of zinc from the
soil.

Two pot experiments were conducted at Santa Fe, Darien Province
of eastern Panama to study the effect of various levels of nitrogen
(N), phosphorus (P), calcium (Ca), and zinc (Zn) on Zn uptake by
jaraguagrass and of P, Ca, and Zn on uptake of Zn by hairy indigo.
To augment the data from the pot studies, six field experiments were
established on jaraguagrass pastures grown on major soil groups in

Darien Province, to the east of the proposed sea-level canal, Route 17.

For the three Panamanian soils used in this investigation, Zn applications had no direct effect on increasing forage yields of jaraguagrass and hairy indigo. Applications of Zn significantly increased Zn concentrations of jaraguagrass forage and crown-root systems in pot studies and showed a positive trend in the field experiments; however, total Zn uptake by forage was significantly increased only by the Zn_2 (30 kg Zn/ha) treatment. All Zn applications increased total Zn uptake by jaraguagrass crown-root systems. Applied Zn significantly increased soil-extractable Zn in all pot experiments. There was an inverse relationship between extractable Zn and applied lime which was expected due to the increase in soil pH.

Zn applied in combination with N significantly increased Zn concentration and total uptake values of jaraguagrass. Lime depressed Zn concentration in jaraguagrass but increased total Zn uptake. Applications of P had no effect on forage Zn uptake or forage concentrations of jaraguagrass and hairy indigo. However, P applications significantly increased total Zn uptake by the crown-root systems. Applications of N up to 50 kg N/ha/harvest significantly increased forage and crown-root yields of jaraguagrass by its beneficial effect on root proliferation and plant growth in general. Lime applications of 2,000 kg Ca/ha significantly increased yields of jaraguagrass on the strongly acid Santa Fe soil. Nitrogen and Ca interactions resulted in increased yields of jaraguagrass. Lime significantly increased hairy indigo forage yields but had no measurable effect on the crown-root systems.

Field studies gave only preliminary indications of Zn concentra-

tion and total uptake of jaraguagrass with Zn and other fertilizer amendments. Forage and soil concentrations of Zn, P, Ca, Mg, Fe, Cu, Mn, and Sr were reported and discussed.

Results indicated that the Panamanian soils studied were inherently fertile and, because of the nature of the colloidal clay fractions, these soils represented an immense reservoir capable of retaining soluble fallout cations against leaching to hydrologic outlets. Application of Ca, in the form of lime, to pastures could reduce total Zn uptake by forage plants.

INTRODUCTION

The Center for Tropical Agriculture of the University of Florida was subcontracted by Battelle Memorial Institute, Columbus Laboratories, authorized under Public Law 88-609, 88th Congress, in 1967 to conduct agricultural ecology studies in eastern Panama and northwestern Colombia. These studies were part of a bioenvironmental feasibility study for the proposed nuclear excavation of an Atlantic-Pacific inter-oceanic sea-level canal (80).

Estimation of the potential external and internal radiation doses to human populations, living in or near the vicinity of radioactive fallout released by nuclear detonation, was the principal objective of the Bioenvironmental and Radiological-Safety Feasibility Program (145). Prediction of the movement of radionuclides in a tropical environment was therefore necessary. A systems analysis approach was used to develop a conceptual bioenvironmental income and loss model. Various biomass compartments and pathways of radionuclide transfer to man had to be defined by sampling and analyzing environmental data. The prime vehicles for the transfer of stable and radioisotopes, food and water, had to be described quantitatively and in terms of activity per unit of food or element for nuclide-intake estimation and internal-dose calculations (125).

Comar (51) observed that the movement of radionuclides in the biosphere could be investigated through two approaches: (a) controlled metabolic studies and (b) assessment of data from surveys. Both of

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these approaches were successfully employed to study the cycling of nuclides through the agricultural ecosystem to man. The investigation reported herein was conceived to provide supplemental information relative to the agricultural ecology project and to generage additional knowledge regarding the mineral interrelations between tropical soils and forage crops.

A reconnaissance survey revealed that livestock enterprises were somewhat recent innovations to eastern Panama although the number of cattle was estimated to be between 7,000 and 10,000 head (79). Higher and more dependable rainfall and the existence of large potential grazing areas are especially advantageous in the production of fattened-beef animals. It is not difficult to speculate, with the acute dietary deficiency of protein in developing countries, the increase in demand for animal products in economically developed areas, and the immense scope for the development and production of pastures and animals in the humid tropics, that the future growth of livestock industry in eastern Panama will be a reality.

Ammerman (5) has stressed the need for a greater understanding of mineral interrelations beginning with those occurring in the soil and in the plant and extending to those occurring at the cellular level of the animal. Mineral nutrition of pastures is an important focal point in the production of forage to meet the needs of the grazing animals, especially in the tropics where the very nature of the climate, soil, and vegetation introduces new problems or variations of those found elsewhere (111).

With the above in mind, one of the essential micronutrients, zinc, was selected for uptake studies by a tropical forage grass and legume

in eastern Panama; partly because of the potential radiation hazard of ^{65}Zn, the neutron capture induced radionuclide, and partly because of the relatively sparse knowledge of its behavior in tropical soils and forage crops and its pathway through the food chain to grazing animals.

Jaraguagrass (_Hyparrhenia rufa_, Nees Stapf.) was chosen as the tropical forage grass in the studies for the following reasons:

(a) it was already established in the proposed study area;

(b) it was valued as a semi-intensive forage crop because of its wide range of environmental adaptability;

(c) it responds to fertilizer applications; and

(d) it would be ideally suited, because of its erect and tufted growth habit, for growth with forage legumes in a mixed sward.

A tropical legume, hairy indigo (_Indigofera hirsuta_, L.) was included in the studies because of its growing importance, especially in a mixed sward, to increase productivity, to provide a cheap source of protein for the animal and nitrogen for the associate grass and its sensitivity to micronutrient levels in the soil (111, 276).

Two pot experiments were therefore conducted at Santa Fe, Darien Province of eastern Panama to study the effect of various levels of nitrogen (N), phosphorus (P), calcium (Ca), and zinc (Zn) on Zn uptake by jaraguagrass and of P, Ca, and Zn on uptake of Zn by hairy indigo. In addition, six field experiments were established on jaraguagrass pastures grown on major soil groups in the vicinity of a proposed sea-level canal, Route 17 (Santa Fe, Patino, and Yaviza) to augment the data from the pot studies. The primary objectives of this investigation were to gain some insight on the interrelationship of Zn with other

macro- and micronutrients in the tropical forage plant and soil, on factors regulating the availability of Zn in the soil and assimilation of Zn by forage plants, and on possible corrective measures in controlling or reducing radionuclide absorption in the event of contamination from fallout.

STUDY AREA

Eastern Panama, Darien Province

The Republic of Panama lies between latitudes $7°9'$ and $9°37'$ north and longitudes $77°9'$ and $85°1'$ west (244). It occurs as an irregular sigmoid land bridge between North and South America with an east to west extension of about 650 km (400 miles) and a north to south extension varying between 50 to 195 km (30 to 120 miles) (39, 103). The land area, including the Canal Zone, is estimated to be 77,882 km^2 (30,062 square miles) (8, 103) and is bisected by a mountain chain varying in height from 60 m (200 feet) at the lowest point to over 3,300 m (11,000 feet) at the high peaks near the Costa Rican and Panamanian boundary (141).

Darien, southernmost province of the Republic of Panama, borders with Panama Province on the northeast, Pacific Ocean on the south, the national boundary between Panama and Colombia on the southeast and is barred from the Atlantic Ocean by Camarca San Blas on the north (103, 222). The province covers an area of about 15,400 km^2 (5,945 square miles). According to Arauz (8), the study area is generally underdeveloped and has a low human population of about 1.8 inhabitants per square kilometer. Most of the population is centered near small towns situated at junctions of the major rivers.

Climatology

The Republic of Panama lies entirely within the tropical belt with mean annual temperatures of 28C in the lowlands and 23C at 610 m (2,000 feet) elevation (39). Higher temperatures are experienced in drier areas along the Pacific coast (103).

Darien Province has an oceanic type of climate with local variations modified by proximity to the higher mountain ranges (222). In general, the region is subjected to high rainfall and humidity and has definite wet and dry seasons (140). Annual temperature variations are small although diurnal ranges of 8 to 11C have been noted in places. These diurnal variations result in considerable early morning cooling frequently compounded with low clouds and ground fog (140).

Orographic concentration of rainfall is pronounced and accounts for the heavy forest cover on windward slopes, especially where they face the sea. The windward (Caribbean) side of the Isthmus which is exposed to the dominant NE tradewinds has a greater mean annual rainfall (over 3,000 mm/annum) and a longer rainy season (about 9 months) compared to a mean annual rainfall of about 1,500 mm and a 7- to 8-month rainy season on the Pacific side (39, 140). This difference has been classically illustrated by comparing the precipitation data of Cristobal, of the Caribbean terminus of the Panama Canal and Balboa Heights at the Pacific terminus (140). Cristobal receives some 3,250 mm of rainfall per year with the maximum falling in November (570 mm). Except for the two relatively dry months of February and March, the remaining months receive approximately 300 mm each. Balboa Heights receives about 1,760 mm per annum with 1,600 mm falling between March and mid-December. A short "dry" spell (Veranillo de San Juan) occurs between July and August.

The 2,000 mm mean annual rainfall in the Darien region is distributed over 8 months of the year from May to December (103, 222). Afternoon and evening showers, often with thunder squalls, seem to be the daily rainfall pattern during the wet season (140).

The relative humidity is generally high in Panama, averaging 80 percent during the wet season (May-December) and 60 percent during the drier season (39). Land breezes are significant along the coastal areas, especially where relief is high (140).

Physiography

Holdridge and Budowski (103) reported that Panama was predominately a country of low to medium elevation with some 76 percent of the total area lying in the tropical basal belt. Eastern Panama varies from extremely flat river bottom lands to steep mountains (146). A range of hummocky hills and low ridges occurs east of Colon and continues southeast along the Atlantic coast into Colombia. In the Darien Province, this range is represented by the Cordillera de San Blas and Serrania del Darien (79, 222). Another range occurring in eastern Panama, Serranias de Maje and del Sapo, extends southward along the Pacific coast into Colombia (147).

The continental divide of eastern Panama lies 8 to 16 km (5 to 10 miles) from the Caribbean coast and extends from the head of the Gulf of San Blas to the Colombian border at Cerro Gandi. It is composed of an arcuate ridge of igneous basement rock which forms the southern escarpment of the Chargres-San Blas graben (244). The divide is convex to the northeast and, for the most part, less than 600 m (1,970 feet) high. The summit of Cerro Tararcuna on the continental divide is the highest point, 1,854 m (6,083 feet).

Bordering the continental divide to the south and southeast is a parallel arcuate lowland which is the continuation of the Pacific coastal plain of Central Panama. The plain is generally less than 90 m (300 feet) in elevation and is drained by the Bayano River basin to the northwest and Tuira-Chucunaque River basins to the southeast. The two basins are separated by an almost imperceptible divide. Terry (143) also observed that the coastal plains and adjacent lowlands are generally wider on the Pacific than on the Caribbean side.

The well-defined drainage pattern of Darien Province is greatly influenced by structure. San Blas range forms a distinct continental divide (79) with the main rivers, such as the Chucunaque, Tuira, Tucuti, Sambui, Balsas, and Sabana, occupying most of the central trough that divides the Caribbean coastal ranges from those of the Pacific side (140). The Caribbean drainage pattern consists of numerous steep and short tributaries draining the slopes of low to moderately high ridges. These tributaries are navigable only along their lower reaches (79). In the Pacific coastal region stream entrenchment is a prominent feature of the landscape. This is typical of areas affected by recent or current uplift. Most rivers draining into the Pacific are not navigable during low tides. Difference between mean high and low tide levels on the Caribbean shore is about 0.7 m (27 inches) as compared to about 6.4 m or 21 feet in the Gulf of Panama (222).

Vegetation

According to Holdridge and Budwoski (103) the natural vegetation of Panama is a result of prevailing climatic and edaphic factors. They identify eight major plant formation zones, four of which are found in

the Darien Province (Fig. 1). Golley et al. (86), describing the
structure of forests in Panama, distinguish four forest types which
are basically similar to the plant formation zones of Holdridge and
Budwoski. The dominant vegetation of the study area is forest with
only small areas under cultivation.

Some 75 percent of the Darien Province is covered by tropical
moist forests composed of an irregular canopy of evergreen trees and
certain emergent deciduous trees, such as the cuipo (Cavanillesia
platanifolia) and bongo (Ceiba pentandra) reaching over 20 to 50 meters
in height. At the onset of the dry season (late December or early
January) leaf fall is greatest. This accounts for the high understory
biomass (leaves and stems of all plants under 2 m height) data obtained
by Golley et al. (86).

The premontane wet forest (86) or the tropical moist forest and
subtropical wet forest (103) occur on mountain slopes at elevations of
250 to 600 meters where the precipitation is highest. This forest is
essentially of the evergreen type with short, dense, and evenly closed
canopies covering abundant epiphytes and lianas which are characteristic
of higher moisture regimes (86).

Holdridge and Budowski (103) delineated a tropical dry forest
transition zone along the upper reaches of the Rios Sabana and
Chucunaque, which Golley et al. (86) identified as gallery forests.
These forests occur on flooded plains or flat lands above the normal
tide levels but are frequently inundated with fresh water. The cativo
(Prioria copaifera) forest is dominant in this area, reaching a height
of over 50 meters and supplying the greatest amount of overstory stem
and litter biomasses (86).

Fig. 1. Plant formation zone of the Republic of Panama.

Source: Holdridge and Budowski (103).

Mangrove swamps and swamp forests are found predominantly along the Pacific high-tide estuarine coast and along the Gulf of San Miguel where tidal level variations are greatest. The tallest and most extensive mangrove forests in the world, composed of pure stands of red mangrove (_Rhizophora brevistyla_), thrive on the periodically inundated tidal areas (140). Where brackish water ends, red mangrove disappears and _Montrichardia arborescens_ (a tall aroid) appears and grows on soft mudbanks (103). Alcornoque swamp forests cover extensive areas above the normal tide levels. The mangrove and swamp forests cover about eight percent of the land area of Darien and have the lowest biomass in all categories examined (86) but high litter and root biomasses. Mangrove prop-roots tend to trap tidal debris.

McBryde (140) observed that very little of the original forest of the Darien remains because of shifting cultivation. The vegetation appears to be mostly secondary growth.

Geology

The Isthmus of Panama probably emerged during the Late Miocene Epoch. Volcanic action, mainly during the Eocene Epoch, resulted in the formation of a submarine ridge from a large deep marine portal which had permitted free interflow of Pacific and Atlantic waters. Uplifting of intensive mountains during the Upper Miocene and Early Pliocene Epochs and further volcanic activity in the Late Pliocene resulted in the land bridge (140).

The geology of eastern Panama has been reviewed extensively by Terry (244), Smith _et al_. (222), and United States Corps of Engineers (255).

A diagrammatic geologic profile of route 17A, located in the Darien Province, is shown in Fig. 2. The highest areas in general are igneous rock remanents while the lower terrain is composed of sedimentary formations with igneous intrusions. The larger part of the basement complex, represented by the Serrania del Darien on the Caribbean side is of basic extrusive igneous rocks, especially andesite and basalt (222, 244). Except for random areas of igneous intrusive rocks, limestone, sandstone, shale, and conglomerates flank and overlie the basement complex of the remainder of the province. The Eocene formation, drained by the eastern tributaries of the Chucunaque River, outcrops along the western side of the divide. It is composed of thick, hard, orbitoidal limestone with sandy and shaly conglomerates and tuffaceous interbeds (244). Calcareous shales and massive brownish marls (with numerous radiolarian spicules and fine volcanic ash) characterize the Oligocene sediments. Radiolarian ooze appears to be more plentiful in the Garachine-Sambu and Tuira-Chucunaque basins while volcanic material is coarser and more dominant in the San Miguel Bay region and is indicative of the shallow terrestrial water conditions during deposition. The Miocene formation, ranging from conglomeratic limestone, shale, and shaly sandstone, to limey sandstone, covers the major portion of central Darien, especially the Tuira-Chucunaque basins. Thicker deposits of conglomerate northwards to Rio Chico suggest delta deposits of a large and vigorous river during the middle Miocene. Younger consolidated sediments of a series of sandstone and shales carrying foraminiferal and other marine fauna are found in the Tuira-Chucunaque basins. These Upper Miocene and Pliocene off-lap deposits together with recent alluvium mark the final withdrawal of the sea from the Darien (244).
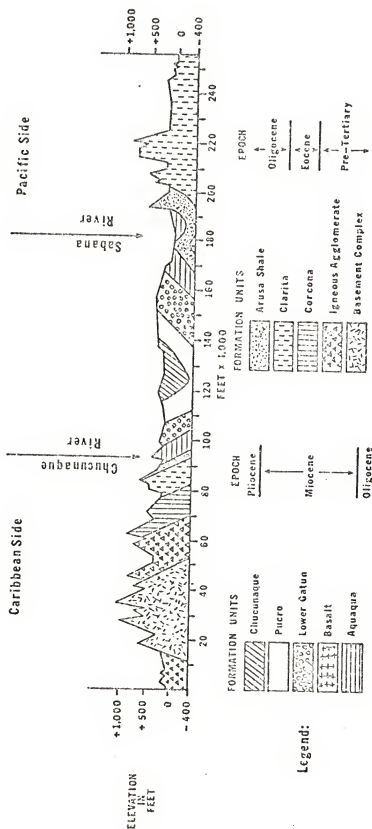
Fig. 2. Diagrammatic geologic profile of Route 17A in eastern Panama.

Source: Taken and modified from U.S. Corps of Engineers (255).

Terry (244) reported that eastern Panama was in a more advanced stage of the erosion cycle, with the wide flats, meandering rivers bordered by ox-bow lakes (as exemplified in the Tuira-Chucunaque basins), and drowned lower valleys. Mountains appear to be in a mature state (244) with evident remains of a peneplain cut by folding, block-faulting of mountains, erosion, and subsequent elevation to nearly 1,800 meters (222). There is evidence of recent isostatic stability (244). Most of the faults are from the southwest to northwest with possible north-south faults caused by asymmetrical folding, overthrusts and faulting of the land mass. The Pirri Range, for example, is an asymmetrical anticlinal fault block which separates the Upper Tuira Valley from the Balsa.

Soils

While specific soil types have been studied in detail by a number of investigators (39, 78, 146, 147, 188, 222, 273) the soils of Panama, especially those of eastern Panama, have been only broadly classified.

Brown and Wolfschoon (39) divided the soils of Panama into four groups on the basis of chemical and physical analyses of representative soil series occurring in western Panama. The groups were latosolic (zonal), hydromorphic (intrazonal), alluvial (azonal) and recent volcanic (intrazonal or azonal) soils. They occupied 80, 5, 10 and 2 percent of the land area, respectively.

Papadakis (175) recognized two broad "soil regions" in Panama, namely kaolinitic ando and tropical mountains-ando. "Soil region" was defined as the pattern of soil formation and distribution and appeared to be basically similar to "soil association." Principal soils of the

kaolinitic ando region include cinnamonic, gleisolic, saline gley (mangrove), ground water laterite, and wet ando. The tropical mountains-ando include cinnamonic, kaolisols, latosolic kaolisols and ando. The diagnostic criteria for these soils seemed somewhat broad and subjective. On the basis of Papadakis' (175) classification, eastern Panama is therefore dominated by the tropical mountains-ando soil region except for the Caribbean draining river basins and coastal areas.

A cursory soil survey of Darien Province was conducted by Smith et al. (222). They considered that topography was the most important soil-forming factor in the Darien and therefore grouped the soils into three catenas; namely, steep hilly uplands, rolling undulating foothills, and lowland areas. The upland catena of mountain ranges and summits was composed of well-leached, stony reddish-brown clayey soils with plastic properties. The low mountain range and hilly upland catena was composed of plastic light reddish-grey clays or, in the depressions, black stiff clays. The lowland catena was subdivided into (a) flood plains and low-lands and (b) tide lands. Alluvial soils included gray plastic clays, gray silty clays, brownish-gray silty clay loam and sandy clay loams while the tidal area soils in and around mangrove swamps were dark grey clays.

On the basis of field and laboratory determinations of samples from 51 forest soil profiles in the Darien, Martini et al. (146) documented three soil groups. They were alluvial, non-latosolic resid-ual and latosolic soils and, in essence, also classified according to topography. Alluvial or lowland soils were derived from mixed sediments of both igneous and sedimentary parent materials and showed the greatest potential for agricultural productivity if protected from flooding above

the brackish water zone. A miscellaneous soil group, the non-latosolic residual, was derived from parent materials of limestones, shales, sandstones conglomerates with some igneous intrusions. This group occupied only a small area but could be successfully cultivated. Latosolic soils, derived largely from basic igneous andesites or basalts, were found to be the dominant soil group but were regarded as suitable only for pastures or forests.

Recently Gamble et al. (78) conducted a reconnaissance soil survey of eastern Panama and Colombia in order to select principal soil types for detailed study. Two soil orders, Entisols and Oxisols, were recognized in eastern Panama (Fig. 3). Oxisols corresponded to the latosolic soil designations reported by Brown and Wolfschoon (39) and Martini et al. (146). Oxisols were found to be the most dominant soil group in the study area. They were generally located in upland areas and were characteristically reddish-brown and red in color and in the acidic range (78). Entisols were subdivided into Psamments, Aquents, Orthents, and Orthents rolling phase which, in general terms, corresponded to beach sands (273), marsh areas (39, 175, 222), alluvial soils (39, 146, 222), and upland, non-latosols (146, 222), respectively. Recent alluvial deposits were regarded as the principle agronomic soils of the sandy area (78). Slightly acid to alkaline pH values, brown, yellowish-brown to strong brown colors, and relatively high levels of plant nutrients characterized the alluvial soils.

The high levels of extractable plant nutrients obtained from selected cultivated soils suggested that the soils of eastern Panama were relatively fertile and that soluble cation losses by leaching were low (78). Clay characterization data have supported this interpretation (85). Clays concentrated from surface horizons of selected

Fig. 3.   General soils map of eastern Panama.

(Inset numbers and circles refer to experimental locations
where 1 is Santa Fe, 2 is Patino, and 3 is Yaviza).

soils showed properties that reflect the tropical nature of these soils. These properties include high percentages of amorphous material, surface area, cation exchange capacity and presence of interlayered montmorillonite-halloysite clay minerals (78). Nuclide retention studies implied that the soil colloidal fraction of Panama clays represented a limitless reservoir capable of retaining soluble radiocations through a surface phenomenon (85).

Agricultural Systems

Eastern Panama, according to Arauz (8), has been dominated by a subsistence economy. Its inhabitants depended primarily upon shifting cultivation, fishing, raising of livestock, hunting, and seasonal gathering of wild fruits. Most agricultural activity was found bordering main rivers and tributaries because of increased soil productivity and ease of water transport.

The principal agricultural exports to Panama City and western Panama were plantain (_Musa paradisiaca_), banana (_Musa_ sp.), rice (_Oryza sativa_), and yam (_Dioscorea_ sp.). Corn (_Zea mays_), bean (_Phaseolus_ sp.), and yucca (_Manihot esculenta_) were produced for local consumption (8, 222). Darien provides most of the plantains consumed in the Province of Panama.

The agricultural systems employed by the different culture groups (Cuna Indians, Choco Indians, Negroes, Mestizos, and Colonialists from western Panama) included (a) shifting cultivation, (b) riverine, (c) plantation, (d) door-yard, and (e) livestock (8, 80).

Arauz (8) contended that shifting cultivation accounted for 70 to 90 percent of the total diet. Snedaker and Gamble (223) identified

two forms of shifting cultivation. Land is cleared of natural vegetation by either the slash-burn or slash-mulch method. Crops are then planted in the nutrient rich ash or debris and continually grown until reduction of yields result in the area being abandoned to forest fallow. Another site is then cleared for cropping. Cultural and environmental factors determine the duration of the intervening fallow periods between cropping sequences and may vary from 4 to 30 years. Fallowing allows the regeneration of vegetation, which in turn immobilizes certain mineral nutrients, conserves soil, and eliminates weeds and other crop pests. Although crop yields are generally low, the system has its advantages from both ecological and anthropic points of view where population per unit area is meager.

Riverine agriculture is practiced to a limited extent on low terraces and other areas subjected to floods during the rainy season. Rice, corn, and beans are planted following flooding (223).

Plantation agriculture is concerned with the production of coconuts, bananas, or plantains. Coconuts are a major source of income for the Cuna Indians (San Blas). The palms are grown along the Caribbean coast and on some islands (8, 78). Choco Indians and negros produce bananas and plantains for commercial purposes. On a small scale, some cacao, citrus, and avocados are grown.

Dooryard agriculture refers to garden plots established close to dwellings. Small livestock such as chickens, ducks, and pigs are reared to supplement the basic diet (78). Covich and Nickerson (52) have described this system as practiced by the Choco Indians.

Livestock enterprises, especially beef cattle production, are becoming commercially important in eastern Panama (8). Immigrant

ranchers from western Panama have initiated this trend of producing fattened cattle for the Panama City market during periods when animals in western Panama are under stress due to prolonged droughty conditions (80). Forests are cleared and, after a crop of rice or corn, improved pasture grasses are sown. Permanent pastures are composed mainly of jaraguagrass (*Hyparrhenia rufa*), guineagrass (*Panicum maximum*), paragrass (*Brachiaria mutica*), elephantgrass (*Pennisetum purpureum*), and some small plots of pangolagrass (*Digitaria decumbens*). Gamble *et al.* (80) reported that three large operators owned most of the present cattle but numerous small operations were developing in the study area. Unofficial counts of 7,000 to 10,000 heads of cattle from Santa Fe, Rio Iglesias, El Real Yaviza, Patino, and Jacque were documented. A few milk cows are kept for local milk consumption and chease production, mainly at El Real, Yaviza, Patino, and Jacque.

LITERATURE REVIEW

Zinc

The name, zinc, comes from German and means "of unknown origin" (189). Although it was described in India in 1597, the Chinese were probably the first to extract Zn metal from brass as a contaminant.

Zinc has been shown to be an almost universal constituent of living matter and is presently considered essential for the growth and normal development of most microorganisms, plants, and animals (189). In a historical review of zinc nutrition, Thorne (246) noted that Raulin in 1863 and 1869 presented evidence that Zn stimulated the growth of *Aspergillus niger* in culture media and Javillier in 1912 and 1914 obtained positive responses from certain crops to applied $ZnSO_4$ and confirmed the need for Zn by *A. niger*. Despite these and other early investigations, Zn was not generally accepted as an essential element until the studies of Sommer and Lipman in 1926 and Sommer in 1928 (246). Although Zn deficiency in plants is overtly dramatic, the causative element was not identified because the symptoms resembled those of diseased plants. In addition, difficulty in freeing nutrient media of traces of Zn thwarted early attempts to establish the essentiality of the element.

Subsequent to the work of Sommer, widespread reports of successful control of Zn deficiency in field and orchard crops through the use of Zn-fertilizers have been well documented. Viets et al. (261) published a list of various crops sensitive to Zn deficiency.

The volume of research work, and hence of literature, on Zn nutrition in plants and reaction in soils is very great and no attempt is made here to review it fully.

Physical and Chemical Characteristics

Zinc has an atomic number of 30 and atomic weight of 65.37. In the periodic table of elements it is in group IIB with cadmium ($_{48}$Cd) and mercury ($_{80}$Hg) and in the chart of nuclides (83) Zn is associated with gallium ($_{31}$Ga) and copper ($_{29}$Cu). The metal has five stable isotopes and eight radioisotopes. Stable isotopes, with their abundance in nature, include: ^{64}Zn (48.89%); ^{66}Zn (27.81%); ^{67}Zn (4.11%); ^{68}Zn (18.57%); and ^{70}Zn (0.62%). Of the eight radioisotopes (^{60}Zn, ^{61}Zn, ^{62}Zn, ^{63}Zn, ^{65}Zn, ^{69}Zn, ^{71}Zn, and ^{72}Zn) only zinc-65, a beta and gamma-emitter with a half-life of 245 days, has been most widely used for biological studies (10, 150).

A bluish-white crystalline metal, Zn is brittle when cold, malleable at 120 - 150C, boils at 920C, and burns with a blue flame to give Zn oxide (ZnO). It corrodes slowly in air to ZnO, displaces hydrogen gas from dilute acids and form zincates with alkali. Zinc is bivalent and exhibits a $+2$ oxidation state in all its compounds (203). In aqueous solution, Zn^{++} hydrolyzes to give slightly acid solutions ($Zn^{++} + H_2O \rightleftharpoons Zn(OH)^+ + H$) and, in the presence of a base in solutions of Zn salts, a white precipitate of Zn hydroxide, $Zn(OH)_2$, may be formed.

Ions of Zn exist in compounds either as a positive radical (e.g. $ZnSO_4$) or as a negative radical or zincate (e.g. Na_2ZnO_2). Since hydroxide is amphoteric, it acts as a base or weak acid depending upon the pH of the liquid environment (246). When a base is added, the hydroxide dissolves to give zincate ions variously represented as

$Zn(OH)_3^-$ or $HZnO_2^-$ and $Zn(OH)_4^=$ or $ZnO_2^=$. The acid zincate form, $HZnO_2^-$, is prevalent in lower concentrations of alkali and alkaline zincate form, $ZnO_2^=$, is the primary form as alkali concentrations increase (203, 246). According to Thorne (246), zincates in alkaline solutions exist in a more complex form since Zn has a coordination number of 6 (Werner's coordination theory). He represented the group as follows:
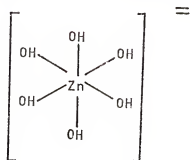
Zinc shows a strong tendency to form stable complex ions (203, 246). For example, $Zn(OH)_2$ dissolves in aqueous ammonia to give a zinc-ammonium complex, $Zn(NH_3)_4^{++}$, and in cyanide solution to form a zinc-cyanide complex, $Zn(CN)_4^=$.

Rice (189) speculated that the rapid reaction of Zn with negatively charged groups may be pertinent to its significance in biology where it is accumulated to higher levels than many elements more abundant in the environment.

The solubility of Zn compounds varies as shown in Table I with selected zinc nutrient carriers.

Zinc Ores

Zinc does not occur in an uncombined state in nature (189). Ores of Zn are widely distributed; the principal one being ZnS or sphalerite. The more common Zn ores are listed in Table 2.

Table 1. Solubility of zinc nutrient carriers.[1]

Compound	Formula	Solubility (gms/100 ml cold water)
Zinc carbonate	$ZnCO_3$	0.001
Zinc chloride	$ZnCl_2$	432.25
Zinc hydroxide	$Zn(OH)_2$	0.26×10^{-8}
Zinc nitrate	$Zn(NO_3)_2 \cdot 3H_2O$	327.30
Zinc phosphate	$Zn_3(PO_4)_2 \cdot xH_2O$	Insoluble
Zinc sulfate	$ZnSO_4$	86.50
	$ZnSO_4 \cdot 6H_2O$	Slightly
	$ZnSO_4 \cdot 7H_2O$	96.50

[1]Compiled from Hodgman, Weast, and Selby (100) and Sauchelli (203).

Table 2. Commonly occurring zinc ores.[1]

Common name	Chemical formula	Common name	Chemical formula
Calamine	$ZnO \cdot SiO_2 \cdot H_2O$	Smithsonite	$ZnCO_3$
Franklinite	$ZnFe_2O_4$	Sphalerite - β	ZnS
Gahnite	$ZnAl_2O_4$	Wurzite - α	ZnS
Goslarite	$ZnSO_4 \cdot 7H_2O$	Willenite	Zn_2SiO_4
Hopeite	$Zn_3(PO_4)_2 \cdot xH_2O$	Zincite	ZnO
Kottigite	$Zn_3(AsO_4)_2 \cdot H_2O$	Zinkosite	$ZnSO_4$

[1]Compiled from Hodgman, Weast, and Selby (100).

Zinc and Soils

Geochemistry of Zinc and Its Relation to Soils

Hodgson (101) suggested that geochemical principals provide a basis for an understanding of elements in soil parent material and thus contribute to the prediction of areas of micronutrient deficiencies and sufficiencies. Mitchell (157) stated that the trace element content of a soil was dependent almost entirely on the rocks from which the soil parent material was derived and on the processes of geochemical and pedochemical weathering to which soil-forming materials have been subjected. Distribution of trace elements in rocks was not generally uniform and the factors governing their distribution have been principally responsible for differences found in soils derived from different parent materials.

Estimated Zn concentrations in the lithosphere have varied from 40 to 80 ppm (84, 189). Igneous rocks were better sources of Zn than sedimentary or metamorphic rocks and in general parent rocks had higher Zn concentrations than soils derived from them. With soil maturity, the Zn content of soils became less influenced by the parent material (101, 157).

Zinc is one of the more uniformly distributed trace elements among igneous rocks formed at various stages of development, remaining approximately proportional to the sum of Fe and Mg (157). Goldschmidt (84) indicated that Zn had a greater tendency to be associated with sulfides (e.g. sphalerite) than most micronutrients. Like Co, Ni, and V, Zn may be enriched in felspars and ferromagnesium minerals when the composition of the residual magma brings about the separation of a sulfide

phase. The bulk of Zn occurs in the more easily weathered minerals of igneous rocks such as olivine, hornblende, augite, and biotite. Since Zn is an important substitute in ferromagnesium minerals, it is found principally in ultrabasic or basic rocks. Zinc occurs in basic rocks at 100-200 ppm and in acid rocks at less than 50 ppm (157).

Although the lithosphere is composed essentially of igneous rocks (about 95%), the surface distribution shows a greater proportion of sedimentary rocks, as they tend to form a relatively thin skin overlying the igneous rocks from which they are derived. Sedimentary rocks of the earth's crust are composed of about 80% shales, 15% sandstones, and 5% limestones. Sandstones are generally composed of minerals that are weathered with difficulty and would tend to produce well-leached soils with low clay and trace element contents. Weathering of shales, especially of inorganic origin, may result in the formation of clay minerals in a medium in which microelements of original igneous rocks are present. Microelements could be occluded or isomorphously substituted in the developing crystal lattice or adsorbed as exchangeable cations. Zinc, Co, Cu, Mo, and B tend to be concentrated in fine sediments. Mitchell (157) reported almost ten times as much Zn in shales as sandstones. Carbonate rocks were found, with the exception of B, to be generally low in micronutrients. Limestones and dolomites had Zn values equivalent to 3-15% of the amount found in the earth's crust. Residual soils derived from carbonaceous material, however, are not necessarily deficient in micronutrients because of the concentration of those elements as a result of weathering. Thorne et al. (248) found that Zn content of calcareous soils in Utah was twice that of non-calcareous soils. Sauchelli (203) noted that limestone soils contained more Zn than do those derived from gneiss or quartzite.

Metamorphic rocks are not abundant in the lithosphere. Pressure and heat to argillaceous sediments result primarily in a recrystallization during which clay minerals are transformed into minerals more closely related to those of igneous rocks. Thermal effects may introduce or remove certain more volatile constituents. For example, Mitchell (157) reported high contents of Zn in Scottish limestone around granite intrusions.

Content and Distribution of Zinc in Soils

In general the total content of Zn in soils is low in comparison with other essential elements (246). An extensive review of literature by Swaine (239) revealed that most mineral soils contained from 10 to 300 ppm total Zn but that exchangeable Zn usually ranged from 0.1 to 20 ppm. Toxic concentrations of Zn from 0.43 to 10.16% of extractable Zn have been recorded in some New York peat soils (228, 229) while values less than 0.2 ppm of extractable Zn have been observed in sandy soils of Alabama (272).

The distribution of Zn in the genetic horizons of soil profiles seems to be related to the degree of profile development or stages of weathering (101). Compared to mature and leached soils, young soils generally have a more uniform distribution of micronutrients in their profiles. Zinc is usually more concentrated in the surface than in subsurface horizons (246). Hibbard (96) observed that the surfaces of undisturbed forest soils were greatly enriched with Zn through decomposition of fallen foliage. Relative to sesquioxides, Wright et al. (289) reported that Zn accumulated in the A_o and B horizons of podzolic and brown podzolic soils and in the A horizons of brown forest soils. It seemed that Zn displayed little tendency to leach and soil

accumulations were closely associated with organic matter residues and processes of podzolization. Higher relative concentrations of Zn in the subsurface horizons may also be caused by impeded drainage which could result in mobilization of the trace element in subsurface gleyed horizons or by mechanical translocation of clay thereby increasing adsorbed Zn in subsurface layers (157).

Variations of Zn have been associated with various soil groups. In South and Western Australia, Stephens and Donald (232) have observed Zn deficiency on calcareous grey soils, black earths, red-brown earths, lateritic podzols overlying sandy parent material, aeolin soils, solodized solonetz soils, rendzinas and others. While Zn deficiencies occurred more commonly on alkaline soils, deficiencies were also recorded on neutral to acid types. Certain tropical soils, such as the acid latosols, showed surface depletion of Zn. Values of less than 2 ppm of extractable Zn were recorded from surface horizons of intensely weathered acid latosols of Hawaii (124). Stukenholtz (237) observed in Nebraska that Zn deficiency in corn was associated in soils which were calcareous, sandy, low in organic matter, heavily graded or eroded such that subsurface horizons were exposed. There have also been reports of high Zn contents in Russian chernozems, which have high clay, organic matter and Ca values, black segregations in krasnozems of Tasmania, and volcanic ash soils and alluvium derived therefrom in Central and Rift Valley Provinces of Kenya (47, 157).

Forms of Zinc in Soils

Few studies have been made concerning the chemical forms in which Zn may be found in the soils, or may assume when added to soils. Early investigations classified forms of Zn in terms of total or insoluble Zn

and Zn extractable by water, acetic acid, ammonium acetate, dithiozone, HCl, KCl, MgSO$_4$, EDTA (ethylenediamine tetraacetic acid), and other chemical reagents or resins and by the fungus, Aspergillus niger. The difficulty of identifying forms of Zn and most other elements in the soil, is apparent in the paucity of relevant literature.

Sauchelli (203) cautiously divides soil Zn into organically combined Zn and Zn in various minerals. Wells (274) postulated the presence of Zn in at least three forms: complexed, exchangeable, and condensed Zn. According to Hodgson (101) there are five theoretical ways in which an element could be bound in soils: (a) associated with soil surfaces, either organic or inorganic; (b) occluded during development of new solid phases in which it is not a principal constituent; (c) precipitated with other soil components, forming a new phase; (d) occupy sites in soil minerals either as an original constituent or by entering the crystal lattice through solid state diffusion, or (e) incorporated in biological systems and their residue in the soil. The distinction between these forms is not usually as precise as the definitions. For example, the demarcation between surface adsorption and precipitation reactions is intrinsically diffuse. Whether the entrance of an ion into microcavities of soil minerals is looked upon as solid state diffusion or surface adsorption is again dependent upon the definition.

Factors Affecting the Availability of Zinc in Soils

The degree of availability of micronutrients in soils is a function of their partition among different forms. Directly or indirectly each form is related to the soil solution through some pseudo equilibrium distribution that is influenced by many factors including pH and supply

and activity of individual soil constituents (101). Regardless of the
total Zn content, soils vary widely in their capacity to supply the
element. For the sake of clarity, the following factors affecting
the availability of Zn in soils are discussed separately although they
are interrelated in the overall effect.

Soil pH and Lime

Numerous investigations have demonstrated that Zn is generally more
available to plants in acid than alkaline soils. Not all Zn deficien-
cies occur on alkaline soils by any means, but the availability of this
element is usually inversely related to soil pH (12, 77, 139, 154, 198).
In general, most pH-induced Zn deficiencies occur within the range of
pH 6.0 to 8.0 (122).

The effect of pH on Zn availability is complex. In addition to
moderating the adsorption or precipitation of Zn in soils, pH may
alter plant uptake of Zn through an effect on microbiological activity,
a change in the ability of the roots to absorb or transport ions to
aerial portions once absorbed, variations in the stability of soluble
and insoluble organic complexes, a change in the solubility of antago-
nistic ions, or an alteration of any rhizosphere effects that may be
present. Also, different plant species respond dissimilarly to changes
in pH and the influence of pH varies with the amount and nature of the
elements present in soils (101).

The strong polarizing ability and hydrophilic nature give the Zn
ion its amphoteric properties. As previously discussed, Zn is a posi-
tively charged ion under acid conditions and is transformed to a nega-
tively charged zincate ion under alkaline conditions. Thorne (246)
postulated that Zn^{++} was the principal ionic form assimilated by plant

roots and doubted whether roots could utilize the ZnO_2 ions which occur under alkaline conditions. DeMumbrum and Jackson (56) found that the ratio of $Zn^{++}:ZnOH^+$ decreased from 1×10^8 at pH 2.0 to 1×10^2 at pH 8.0.

The effect of pH could also result from the differences in solubility of various pH-dependent forms of Zn occurring in the soil (56, 61, 122, 203). Jurinak and Thorne (122) titrated ^{65}Zn-bentonite suspensions (with ^{65}Zn adsorbed to 0.5, 1, and 2% of the exchange capacity) with hydroxides of different cations. Zinc solubility reached a minimum in the pH range of 5.5 to 6.7 in both the sodium and potassium systems. As the alkalinity increased beyond pH 7.0, the solubility increased. With calcium, Zn solubility reached a minimum at pH 7.6, and no increase in solubility was recorded as pH of the system was increased. It appeared that slightly soluble $Zn(OH)_2$ was formed near the neutral pH range and the soluble Na- and K-zincates and slightly soluble Ca-zincate were formed over the alkaline pH range.

According to Sauchelli (203), the solubility values established for certain Zn compounds help predict the availability of Zn at different pH values. The low solubility values of $Zn(OH)_2$ and $ZnCO_3$ suggest that soils having a high pH value would usually contain relatively small amounts of available Zn. When Zn is added to soils having a relatively low pH or a relatively high concentration of nitrate-, chloride-, or sulfate-containing fertilizers, the supply of soluble and available Zn would increase but over a period of time could bring about a depletion of indigenous supply of available or exchangeable Zn through leaching. Jackson et al. (116) revealed that the level of water-soluble Zn decreased as pH of the fertilizer system increased

when $ZnSO_4$ or $Zn(OH)_2 \cdot ZnSO_4$ was applied. From the work of Stewart and Leonard (1956), Hodgson (101) reported that the maximum $ZnSO_4$ uptake added to soil was at pH 4, but the maximum uptake of applied Zn EDTA was at pH 7. It was assumed that Zn fixation was predominant at pH values above 4 where $ZnSO_4$ was added, but where EDTA was added Zn was not fixed and was more effectively utilized by the plant at higher pH values. The amounts of Zn extracted with chemical solvents may vary more with soil pH than the amounts removed by plants, presumably due to the greater efficiency of nutrient absorption by plants at higher pH values. Complexing effects of soluble organic matter were suggested by Camp (42) as the possible reason for the relative insensitivity of Zn uptake by plants changes in soil pH.

Many workers have reported a decrease in available Zn or plant uptake of Zn with lime applications to the soil, especially acid sandy soils (28, 154, 198, 213, 214, 271, 290). Zinc deficiencies have also been observed in calcareous soils (144, 164). In addition to the pH effect of lime additions to the soil, calcium carbonate may act as a strong adsorbent for Zn. This phenomenon will be discussed later.

Soil phosphate

Results reporting the effects of phosphates on soil Zn availability have been conflicting. Soils high in soluble or total phosphates or which have received high rates of phosphate fertilizer have frequently been observed to cause Zn deficiency in crops and Zn unavailability (48, 81, 124, 178, 180, 198, 208, 209, 210, 213, 225, 246). Several workers have also reported that phosphates have either no effect or a beneficial one (26, 27, 90, 118, 167, 246, 260). Shukla (213) observed in laboratory experiments that KH_2PO_4 and $(NH_4)_2HPO_4$ actually increased the availability of Zn in incubated soils.

Stukenholtz (237) established that the reduction of available Zn in soils with high phosphate supply was accentuated in older and neutral calcareous soils and in soils indigenously low in Zn. In sandculture studies, Pauli et al. (177) revealed that excess $CaCO_3$ increased ^{32}P and decreased ^{65}Zn translocation from the roots to leaves of beans. Although excess $CaCO_3$ reduced water-extractable Zn and P in the growing medium, high P treatments increased the water-extractable Zn. They deduced that the P-Zn interaction was within the plant. Various theories have been postulated as to the site of the P-Zn antagonism. The general consensus of opinion is that the P-Zn inter-action occurs physiologically within the plant (24, 237), especially within the roots or conducting tissues where the mobility or solubility of Zn may be reduced (21, 41). Using a split-medium technique, Boawn and Brown (24) showed that while high levels of applied P induced chlorosis and stunting, Zn content of plants was not decreased. Re-sults indicating that normal metabolism was dependent upon a physiolog-ical P-Zn relationship were demonstrated by Paulsen and Rotimi (178) who could not correct the low content of Zn in a P-sensitive variety of soybean, grown in a high P nutrient solution, by addition of $ZnSO_4$. The P-tolerant variety submitted to the same treatment responded to the Zn amendment. Interaction of P with Zn decreased Zn concentration of the leaves most and roots least. It appeared that the effect of P on Zn originated in the roots and occurred on translocation to the upper plant parts.

Bingham (21) contended that the P-Zn interaction was not exclu-sively involved within the plant and that reactions outside of the physiologically active root contributed to P-induced Zn deficiency.

Most investigators have discounted the theory that Zn may be directly precipitated by phosphate ions despite the reported low solubility values of Zn-phosphate compounds (126, 237, 247).

Thorne and Wiebe (247) believed that there was a distinct possibility that Zn may be strongly adsorbed on surfaces of phosphate minerals in the soil. Fulvic acid-Zn-phosphate complexes in the soil have recently been studied by Schnitzer (207).

Nitrogen

Reports generally indicated increase in Zn availability or Zn uptake by plant when nitrogen fertilizer was applied (76, 154, 161, 180, 213, 225, 237). Reasons for this observation are diverse. Miller et al. (154) suggested that N stimulated plant growth and extension of a root system which would tap a wider soil area. There is no direct physiological interaction between N and the deficient element. Most workers have recognized the pH effect on soils of various nitrogenous fertilizers. Acidic N-fertilizers, such as $(NH_4)_2SO_4$ and NH_4NO_3, were found to decrease soil pH and thus increase the availability of indigenous and applied Zn to plants (213, 237). Viets et al. (262) noticed that $NaNO_3$ actually decreased Zn uptake by plants, presumably because of the negligible effect of the fertilizer on soil pH.

According to Thorne (246), negative effects of nitrogenous fertilizer applications on Zn absorption have also been documented by many investigators. Regardless of the N source, Ozanne (173) recorded a severity of Zn deficiency in clover plants grown on soils low in Zn. A significant negative correlation was found between Zn concentration in the tops of subterranean clover and percent protein N. It was concluded that Zn was rendered immobile in the root by forming a metallo-

organic complex with protein under conditions of high nitrogen and low Zn. Other factors, notably pH, were not considered. Williams (282) considered that N may be expected to accentuate a micro elements deficiency because the resultant increase in growth will increase the demands which the plant makes on a limited supply, even if there is not direct physiological interaction between N and the deficient element.

Other cations

Inverse relationships have been documented for Zn and Cu (59, 155, 232) Zn and Mn (1, 65, 113), and Zn and K (180). Whether these antagonisms occurred in the soil and soil solution phases or in the rhizosphere and plant phases was not clearly ascertained. Zinc has been observed to interfere with Fe uptake and metabolism in plants but the reverse was not true (109, 115, 133, 215).

Barrows and Gammon (14) reported a complementary effect of Zn on Mg in the soil and within the roots of tung trees but found a negative interaction at the root-soil interface. The antagonistic Zn-Mg reaction was presumed to be a result of competition for exchange sites.

Zinc sources

Zinc compounds of both high and low water solubility have been found suitable sources of Zn for plant growth when applied directly to the soil (27, 42). Water-soluble compounds include, $ZnSO_4..xH_2O$, $ZnSO_4.$ $(NH_4)_2SO_4.6H_2O$, $Zn(C_2H_3O_2)_2.H_2O$, $ZnCl_2$, polyflavanoid Zn (Rayplex Zn), and the Zn chelates ($Na_2ZnEDTA$, $NaZnHEEDTA$, $ZnDTPA$, and $ZnNTA$, etc.). Slightly soluble sources include ZnO, $ZnCO_3$, Zn frits, and some Zn phosphates. Soil application, foliar spraying of liquid or suspensions, injections into tree trunks, and driving Zn-coated nails or pieces of

galvanized iron into the trunks and limbs of trees have all been used as corrective or preventative treatments for Zn deficiency (48, 246). The degree of success has varied depending upon the Zn source, crop, soil, and climate.

Soil application of Zn fertilizers is the most popular method and may last several years, again depending upon soil conditions, plant uptake, and management. Foliar sprays are generally only effective for the current crop and may have to be reapplied more than once during the cropping season to correct Zn insufficiency. For most annual crops, foliage spraying is considered an emergency treatment.

Reports on the effectiveness of various Zn sources have been diverse. Wallace and Romney (267) concluded from their literature review and findings that chelated sources of Zn were generally about five times as effective as inorganic sources in overcoming Zn deficiency. Chelated Zn sources were more effective than $ZnSO_4$ at low application rates for the growth of corn. Soils treated with ZnEDTA were found by Judy (119) to contain higher water-extractable Zn than those treated with $ZnSO_4$ which appeared to be fixed rapidly in the soil. Norvell and Lindsay (170) claimed that ZnEDTA was most stable in the soil suspensions near neutrality. Not all workers, however, agree that Zn chelates are more effective than inorganic Zn sources (214, 246).

Since Zn is often added to mixed fertilizers, the extent to which manufacturing procedures, storage, and soil conditions modify the solubility of added Zn and the relative agronomic value of the source are important considerations. Nikitin and Rainey (167) reported that the level of water-soluble Zn was higher when $ZnSO_4$ was mixed with acid-forming superphosphate than with a nonacid-forming 6-4-6 compound fer-

tilizer which had been ammoniated. Jackson et al. (116) found that the level of water-soluble Zn from inorganic sources ($ZnSO_4$ and $Zn(OH)_2 \cdot ZnSO_4$) decreased as the pH of the fertilizer system increased whereas chelated Zn remained water-soluble in all of the fertilizers treated.

In Michigan studies, both level of water-soluble Zn and Zn uptake were higher when $ZnSO_4$ and ZnEDTA were coated or hand mixed with fertilizer rather than incorporated during manufacture (64). Richards (195) determined the effect of incorporating various Zn sources into an 8-16-8 granular mixed-fertilizer before and after ammonification and as a coating. Most of the Zn from chelated sources remained in a water-soluble form for all methods of incorporation. When incorporated prior to ammonification, the water-soluble fraction of the soluble Zn sources was less than 10%, but increased progressively for the incorporation after ammonification and coating treatments. Coating fertilizer granules with basic Zn compounds of low solubility increased the level of water-soluble Zn. He concluded that coating was the best way to provide water-soluble Zn in fertilizers and that chelated Zn was the most satisfactory material to use.

Crop response to Zn was generally greater when $ZnSO_4$ was applied with N than with P fertilizers (161, 262). The quantity and species of Zn compounds precipitating in fertilizer residues were influenced by the pyrophosphate content and pH of ammonium phosphate mixtures (40, 107). At pH values below 4.0, the quantity of Zn in the residue increased with increasing pyrophosphate content. All of the Zn precipitated in the orthophosphate systems at pH 5.0 and above. More Zn moved out of the pellet when pyrophosphate levels were increased, especially with

increasing pH. Precipitation of Zn was minimum when the pyrophosphate content of the ammonium phosphate was between 40 and 80%. Growth chamber studies revealed that Zn uptake of applied Zn was inversely proportional to the quantity of Zn precipitated at the site of placement.

Mixing Zn sources with the soil was generally found to be more effective in supplying Zn to plants than band applications (36, 161, 212). Chelated Zn was often more effective when band-placed than inorganic Zn because of its greater mobility in the soil. However, band-applied granular $ZnSO_4$ was observed to be equally effective, especially when blended with granular macronutrient fertilizers. Apparently uniform distribution of applied Zn in the soil is essential for maximum effectiveness. Liquid fertilizers proved to be more effective carriers of Zn than granular fertilizers when ZnO was the Zn source (159).

Several workers have reported that alfalfa cover crops in orchards have reduced or prevented Zn deficiency symptoms (48, 59, 246). The beneficial effects of alfalfa on Zn availability in soils have been attributed partly to the deeply penetrating roots bringing Zn from lower horizons to the soil surface, followed by top decomposition and subsequent Zn release. Alfalfa may directly increase available Zn supply to plants growing in association with it. Millikan (155) suggested that alfalfa roots might solubilize Zn in the soil. Alfalfa, like most legumes, contributes a significant amount of N to the soil through decomposition of its root-nodules. The possibility of an indirect effect of N to subsequent crops cannot be discounted.

Rasmussen and Boawn (186) evaluated Zn uptake by bean plants from

Zn materials ($ZnSO_4$, ZnEDTA and Zn polyflavonoid) applied to the seed coat as a substitute for Zn fertilization and as a means of eliminating temporary early season deficiency. The seed treatment was not sufficient to meet the plant needs beyond the three-compound-leaf stage of growth even though the amount of Zn applied through seed treatment exceeded total Zn uptake requirements for the entire crop cycle. In conjunction with Zn fertilization, Zn seed treatment did eliminate early season deficiency symptoms.

Adsorption by clay minerals

Various soil colloids have been found to adsorb Zn and thereby reduce, to varying degrees, the availability of the element. Hibbard (96) postulated the importance of the clay fraction in providing the necessary large surface area for trace element adsorption. Many workers (12, 95, 105, 211, 249) have successfully related Zn content of soil to its clay content. Wahhab and Bhatti (265) graphed Zn contents of 32 Pakistan soils against clay content and found a marked curvilinear relationship. Sand and silt fractions have also been observed to fix Zn but this may be due to their association with soil organic matter (95, 105).

Zinc is not adsorbed on all clay minerals by the same mechanism. Electrostatic forces giving rise to cation exchange reactions attract Zn as they do all soil cations, but the interaction of Zn with clay (and organic) surfaces involves additional forces of attraction, generally termed specific adsorption (101, 211, 249).

Elgabaly and Jenny (61) ascertained that the adsorption of Zn by montmorillonite from $ZnCl_2$ solution involved Zn^{++}, $ZnCl^+$, and $ZnOH^+$ but only the divalent fraction could be removed with neutral salts. They

concluded that the nonextractable Zn had entered the octahedral layer of the crystal lattice. Further support for the fixation of Zn in clay lattices was revealed by Nelson and Melsted (165) who added $^{65}ZnCl_2$ to soils and clay suspensions and measured the removal by plants and various extracting reagents. The data indicated that Zn retention by soils had the following relation to other cations: H > Zn > Ca > Mg > K. Neutral salt solutions removed only part of the adsorbed Zn from the soils and clays while acidified solutions remove most of the remainder. It appeared that the Zn removed by acid, but not by the neutral salt solutions, had no significant effect on the cation exchange capacity and neither did it replace exchangeable cations such as Ca. Thus non-exchangeable or acid soluble Zn was not considered to occupy exchange sites and the proportion of Zn adsorbed in this manner was observed to increase with increasing length of time of contact between soil and Zn solutions and with the degree of Ca saturation of the soils or clays. From infrared absorption studies on montmorillonite, DeMumbrum and Jackson (54) indicated that Zn and Cu reacted in part with OH groups in the silicate layers of the crystal lattice. They took the position that the fraction of the exchange capacity was specific for Zn and Cu. The same investigators (55) later showed that Ca-montmorillonite and Ca-peat accumulated Zn ions from dilute solutions in equilibrium with relatively insoluble compounds as $Zn_3(PO_4)_2$, and ZnO. This again illustrates the strong adsorption of Zn on clay colloids and partly accounts for its low solubility and availability observed in some soils.

Mineral surfaces vary widely in their reactivity with Zn. Elgabaly (60) disclosed that Zn adsorbed by bentonite, kaolinite,

pyrophillite, muscovite, biotite, vermiculite, brucite, and talc was not all replaced by ammonia. He assumed the non-exchangeable Zn as being adsorbed in unfilled holes in the octahedral layer of alumino-silicates. Zn fixation by clays with low Si/Mg ratios, such as magnesium, bentonite, vermiculite, and brucite, did not decrease ammonia adsorption capacity. This implied that Zn may have replaced magnesium ions in the exposed lattices of the clay particles. Working with Zn at concentrations within the solubility of $Zn(OH_2)$, Jurinak and Bauer (121) studied the adsorption of ^{65}Zn on calcite, dolomite, and magnesite minerals. The order of the strength of Zn adsorption was magnesite> dolomite > calcite. Thermodynamic evidence showed that the reaction of Zn with calcite was distinctly different from the inter-actions with dolomite and magnesite. The possible substitution of Zn for Mg in crystal lattices of dolomite and magnesite was postulated, especially since the ionic radii of the two ions are similar: 0.83 and 0.78A for Zn and Mg, respectively. In addition, entropy data supported the concept that Zn was stripped of water of hydration on being ad-sorbed by dolomite and magnesite but such an energy change did not occur on adsorption with calcite.

Zinc deficiencies have been observed on calcareous soils and excessively limed acid soils (253, 271, 285). An inverse relationship between indigenous Zn absorption by tomato plants and soil $CaCO_3$ content was recognized by Navrot and Ravikovitch (164) in an investigation of soils originating from a homogenous carbonaceous parent rock. Absorption of Zn by plants was also observed to be reduced with in-creased levels of less than 2u particles of $CaCO_3$ or carbonate clay. Adsorption of Zn with the carbonate mineral was suspected.

Hodgson (101) reported that in 1952, Gibbs and Marshall have shown that the surface of feldspars in contact with an aqueous solution alters to give a porous zeolite-like structure that grades into the normal feldspar crystal with increasing distance from the surface. Removing this layer from the felspar by treatment with base, Tiller (249) noticed a mark reduction of Zn and Co adsorption. The same treatment did not affect the adsorption of these elements by clay minerals not expected to have this relatively amorphous layer.

Tiller (250) recently advocated that silicic acid in soil solution may have an important role in reactions controlling the availability of micronutrients. The amount of Zn adsorbed by montmorillonite and kaolinite clays increased with increasing amounts of silicic acid adsorbed, especially at low soil pH and Zn concentration. Results indicated that adsorbed silicic acid provided additional adsorption sites on the clay only. In situations of high local Zn concentration or in very alkaline soils, Zn was postulated to be precipitated into silica-containing compounds.

Organic matter

The relative influence of soluble and insoluble organic compounds and their relation to inorganic soil constituents in a mineral soil is yet to be clarified. Positive correlations between Zn content of the soil and soil organic matter have been noted by some workers (12, 143, 166). Organic matter may promote the availability of certain elements, presumably by supplying soluble complexing agents that counteract fixation. At the same time, soils that are most commonly deficient in Zn and fix the greatest quantity of this element are organic in nature (101).

Humic (acid-insoluble) and fulvic (acid-soluble) fractions of the soil organic matter have appreciably contributed to the adsorption and complex formation abilities of the soil. Processes involved in reactions between Zn and organic matter have been attributed to ion-exchange, surface adsorption, coagulation, complexation, chelation, and precipitation (128, 166).

The significant contribution of the cation exchange capacity of many soils by organic matter is well known. Baughman (17) furnished evidence that Zn was associated with organic matter in chelated (Cu-acetate-extractable) and complexed (released by oxidation of organic matter with H_2O_2) forms. Infra-red absorption studies with peat (54) confirmed the chelation-type reaction and showed considerable shifts in the double-bond region of peat in sorbing Zn and Cu which were not apparent when Ca and other basic cations were sorbed. It appeared that functional groups in organic matter involved weak acids, the configurations of which offered opportunity for chelation of heavy metals.

Broadbent and Bradford (33) revealed by methylation that carboxylic and phenolic groups and H^+ attached to heterocyclic compounds seemed to be the more important exchange sites. These groups probably occurred on certain lignin side chains, amino acids, and tannins, and heterocyclic N in nucleic acids. Randhawa (185) methylated humic acid and revealed that Zn^{++} was retained mainly by carboxyl and mildly acidic phenol groups. Some 75% of the Zn bound to humic acid was exchangeable with NKCl while the remainder could only be desorbed by $0.01N$ HNO_3 and a small portion by $0.1N$ and $N$$HNO_3$. Both monovalent and divalent forms of Zn were adsorbed by the humic acid complex; however, the relative proportion of the specific sites was pH dependent. As pH increased

from 3.6 to 7.0, the monovalent Zn adsorbed decreased from 75 to 30% of the total adsorbed Zn. Stability constants of Zn-humic acid complexes at pH values of 3.6, 5.6, and 7.0 were given as 4.09, 6.31 and 7.22, respectively and were much lower in value and therefore less stable than Cu and Fe-humic acid complexes.

Recent interest has centered on the fulvic acid fraction of the soil humic acid complex. The importance of fulvic acid in the supply and availability of Zn and other cations in the soil was demonstrated by Henry (95) who recorded that over 70% of the added ^{65}Zn with ground alfalfa was initially found in fulvic acid and water-soluble fractions. This amount declined rapidly to about 20% after 20 weeks of incubation. The decrease of Zn content of fulvic acid and corresponding increase of Zn in the mineral fraction indicated the formation of an organo-mineral gel which was responsible for increased Zn adsorbed by the mineral fraction. Zinc was not observed to move from the fulvic to the humic acid fractions. According to Schnitzer (207) podzol fulvic acid was a highly oxidized, biologically stable, and water-soluble naturally occurring complexing agent. The acid complexed metal ions and hydroxylated metal compounds with phosphate interacted with clay minerals and at concentrations over 500 ppm demonstrated a positive effect on root initiation of bean stem segments. Stability constants of Zn-fulvic acid complexes increased with increasing pH and, with the exception of Mg, were found to be higher than all other metal fulvic acid complexes.

In a preliminary Rothamsted study, Mitchell (157) reported that Zn and other trace elements may be adsorbed or coprecipitated with iron and other oxides, especially in soils derived from sedimentary parent

material which has passed through several weathering cycles. Sand grains coated with iron oxide had the same adsorptive effect. However, under anaerobic conditions and in the presence of fermenting plant material, appreciable mobilization of Zn was evident.

Addition of organic supplements to soils, while commonly increasing the extractable form of an element, may not necessarily increase its availability to plants. Miller and Ohlrogge (152, 153) have shown that water extracts of manure and other organic residues solubilized Zn in soil but Zn absorption by plants was reduced. Decomposition or humification of added organic sources such as alfalfa, sugar beet tops and manures have been found to inactivate Zn over a period of time from water-soluble to non-exchangeable forms which were less available to plants.

Wallace (266) has comprehensively reviewed the importance of soluble chelating agents, both natural and artificial, in rendering and keeping ions stable in the soil solution. This has led to new evaluations of the significance of organic matter in affecting micro-nutrient availability.

Microorganisms

The effect of microorganisms on the availability of Zn and other micronutrients is principally through the release of inorganic ions during decomposition of organic materials and through immobilization of ions by incorporation into microbial tissue. Zinc deficiency in corn and fruit trees (little-leaf disease) has been alleviated by sterilization of the soils with formalin, steam, or ether or by the addition of $ZnSO_4$ (246). The deficiency was assumed to be aggravated by microorganisms since the deficiency symptoms redeveloped by inocu-

lation with a small amount of untreated soil. Whether sterilization of the soil actuated the breakdown of nonabsorbable Zn complexes into available forms, reduced competition for available Zn, or altered the pathological interaction has not been established. Allison (4) observed that ethylene oxide sterilization increased water-soluble organic matter and soil pH. There was a possibility that enzymes liberated during the sterilization process continued to degrade organic compounds to form, among other things, soluble complexing agents.

Physiological aspects account for variations of elemental content of different plant species growing in the same media. Another factor affecting the absorption of nutrients by plant is associated with the rhizosphere. Plant roots are known to exude many compounds in sufficient quantities to alter the chemical properties of the rhizosphere either through their influence on microbial activity or through a direct interaction with elemental soil constituents (101). Elgawhary et al. (63) recently developed a laboratory cell to simulate the release of root exudates into ^{65}Zn-labelled soil and to measure the diffusion of complexed ^{65}Zn into simulated roots. They concluded that exudation, complexation, and return diffusion of the complexed metal increased their transport and availability in the soil.

Mobility and diffusibility of zinc in soils

Mobility of an element in soils is a reflection of its solution concentration as it is affected by the movement of water through the profile (101). As such, any factor that affects the solubility of an element, and hence its availability to plants, must in some way affect its movement.

Inorganic Zn amendments do not generally move far in the soil

profile. Brown et al. (37) showed that applied Zn as $ZnSO_4$ and ZnO remained in the surface inch of soil even after leaching with 3 feet of water. They reported that even though the Zn was retained in a water-soluble form in the soil studied much of it was removable with a dithizone extract. Barrows et al. (15) recorded little lateral movement of Zn in soils of Florida and that movement was primarily towards rather than away from tung trees. Highest rates of movement were found on soils low in organic matter, P, and clay minerals other than kaolinite. Fiskell et al. (72) stated that the major effect of fertilizer P on Zn fertilization within moist fertilizer caused soluble Zn to become insoluble and this suppressed Zn mobility. Soluble P, however, did not prevent Zn diffusion from occurring in sandy Florida soils. Mortvedt and Giordano (160) examined the movement of Zn from granules containing 2% Zn as $^{65}ZnSO_4$ in acid soil and found that Zn movement decreased in the following order: ammonium nitrate > soil (no carrier) and concentrated superphosphate > monoammonium phosphate and triammonium pyrophosphate. In limed soil Zn movement was less from monoammonium phosphate than from all other carriers, and Zn movement from each carrier was less than that in acid soil.

Soluble organic compounds, such as organic chelates, have been found to promote the movement of Zn and other heavy minerals in soils. Jones et al. (118) demonstrated that ^{65}Zn, when added to soil columns, moved downward only when either alfalfa extract or CO_2-saturated water was added. But applications of $CuSO_4$, superphosphate and the equivalent of several years of rainfall did not mobilize Zn from the surface of the soil. The contribution of chelating agents to the movement of Zn in soil was studied by Elgawhary et al. (62) who found that the apparent

diffusion coefficient of Zn increased 25-fold when EDTA was added to the soil. This increase was explained by the transformation of ^{65}Zn-exchangeable Zn (labile form) to soluble ZnEDTA complexes thereby increasing the total concentration gradient of diffusible ^{65}Zn. Another study by the same authors (63) on the effect of complexing agents and acids on Zn diffusion to a simulated root system was described under the microorganism section of this review. These investigators concluded that chelating agents, either natural or synthetic, played an important role in eliminating the rate-limiting step of diffusion which hampers the movement and the uptake of Zn and other micronutrient cations by plants growing in soils.

Clarke and Graham (50) determined the Zn diffusion and distribution coefficients of Zn in soil as effected by soil texture, Zn concentration and pH. The diffusivity of ^{65}Zn (K_{Zn}) added to a loam soil (pH 5.0) increased five-fold when the concentration was raised from 0.5 to 4.3% of the soil's cation exchange capacity. Similar values for sand and clay were obtained due possibly to similar mineral clay composition. It was inferred that preferential adsorption of Zn by soil colloids occurred at low Zn concentration but further Zn additions rendered Zn more mobile. Hence Zn diffusity may be enhanced by high local concentrations near fertilizer granules or reduced in zones of Zn depletion that may develop around absorbing roots. Diffusion was also highly dependent on soil reaction. At pH 4.5-5.0 the K_{Zn} values were 2-3 x 10^{-7} cm^2 sec^{-1} whereas values measured at pH 7.2 to 7.5 were less than 1 x 10^{-8} cm^2 sec^{-1} and were comparable with those of phosphate. At higher pH values the precipitation of $Zn(OH)_2$ and, eventually, $CaZnO_2$ were likely possibilities. These changes resulted in a sharply

reduced mobility of Zn in soils. It was also speculated that at high
pH the uptake of Zn by plants would be limited by its rate of transfer
to root surfaces, since under these conditions transfer both by diffu-
sion and by convection in the transpiration stream would be slow.
Values for the distribution coefficients, which is the ratio of the
concentration of solid phase or reacted Zn to the concentration of an
equilibrium Zn solution, decreased as soil Zn concentration was raised
and increased with higher pH values. It was assumed that preferential
adsorption of Zn by soil colloids produced a non-linear adsorption
isotherm, a conclusion also indicated by Nelson and Melsted (165).

Seasonal and climatic variations

There is considerable divergence of conclusions regarding the
effect of season and climate on soil availability of Zn and other
micronutrients. Considering that seasonal changes involve variations
in microbial activity, moisture, and temperature which in turn modify
many other factors, ranging from organic matter supply to the evapo-
transpiration rate, the anomalous interpretations are understandable.
Similarly, the effect of changes in weather patterns on plant composi-
tion and relative uptake of nutrients also involves such factors as
light intensity and duration, stage of growth, and rate of growth (97).

Cool, wet conditions were generally conducive to Zn deficiency
in various plants (1, 59). Hoyle (108) noticed that Zn availability
increased during the summer with peak levels in mid-June and gradually
declined to the lowest Zn values in yellow birch leaves during May.
The deficiencies were often temporary and disappeared as the growing
season progressed.

The complementary relationship between soil temperature and Zn

availability or Zn uptake by plants have been well documented (16, 65, 81, 174, 210, 268). Bauer and Lindsay (16) advocated that increasing soil temperatures from 62 to 86F effectuated a change in the metabolic processes of corn plants, induced root growth and root proliferation which in turn resulted in greater Zn uptake per unit weight of root. Ganiron et al. (81) concluded that temperature affected Zn availability more than uptake or translocation in corn. Despite low relative temperatures, Sharma et al. (210) discovered increased Zn contents in roots of rice with Zn applications but detected no significant translocation to the leaves.

Ozanne (174) showed that subterranean clover absorbed more Zn during long days than short but retained relatively more in their roots. Increased light intensities depressed Zn concentrations in the leaves; the total amount of light received was found to be more important than either light intensity or day length alone. More detailed analyses of data by other workers have also revealed other modifying factors that may have influenced the availability of Zn and behavior of the plants. The optimum temperature range for Zn absorption coincided with optimum mineralization of soil N and P (16). Although no Zn deficiency symptoms were observed in greenhouse-grown corn by Stukenholtz (237) during winter and fall, it appeared that the pH depression caused by acidic fertilizers was more likely to have increased Zn uptake than the low light intensities and higher temperatures.

Miscellaneous factors

Lal and Taylor (130, 131) investigated the effects of constant water-table depths and intermittent flooding on nutrient uptake of corn in lysimeter and growth chamber environments. Shallow water-table

depths and intermittent flooding decreased Zn content of corn and
extractable Zn. Leaf Zn contents for 15 cm, 30 cm and no water-table
treatments were 72, 82, and 92 ppm, respectively. Increased depth to
water-table or improved drainage increased Zn uptake. Nutrient uptake
by plants under wet soil conditions was obviously affected both direct-
ly and indirectly by soil and plant factors. Reducing conditions in
the soil could be associated with increased solubility of heavy miner-
als such as Al, Fe, and Mn which in turn may coprecipitate Zn, convert
nitrates to ammonia, lower soil O_2 and increase soil CO_2 contents,
decrease pH, lower soil temperature, and change microbial activity.
Wet soil conditions also involve physiological and morphological
changes within the plant such as inhibition of root growth and spread,
suberization of root hairs in a high CO_2 rhizosphere environment, re-
duction of Zn translocation and other phenotypic changes.

Recently Rudgers et al. (200) noticed that atrazine (a triazine
herbicide) increased Zn contents in leaves and culms of corn grown on
Zn-deficient soils, especially during early growth and under low soil
temperatures.

Zinc Nutrition of Higher Plants

Function

The most prominent role of Zn in higher plants appears to be its
interrelationship with auxin, a plant growth hormone (163, 246). Work
with Zn-deficient tomato and sunflower plants led Skoog (216) to dis-
cover that auxin activity in stems was negligible and in leaves was
very much reduced. A growth depression was noted in Zn-deficient plants
after a reduction of 50% or more in auxin content. Addition of Zn to

severely deficient plants resulted in an increase in auxin content within 24 hours. Tsui (251) confirmed Skoog's findings and observed that the decrease in auxin of Zn-deficient plants applied to both bound and free auxin. He furnished evidence that Zn was implicated in the synthesis of auxin by way of tryptophan, the content of which was low in the Zn-deficient tomato plants studied. It was concluded that Zn was required directly for the synthesis of tryptophan and indirectly for the synthesis of indole-3-acetic acid (auxin) by oxidative deamination of tryptophan. Wildman et al. (279) have shown this process to be enzymatically activated.

Leaves of Zn-deficient tomato plants were found by Tsui (252) to be lower in moisture content than normal leaves. This observation was incident to the reduction in auxin content. In a review paper, Thorne (246) reported that auxin in plants was apparently responsible, under aerobic conditions, for loosening the cell wall which permits uptake of water into the cell wall. Diez-Altares and Boroughs (58) studied the intracellular localization of ^{65}Zn in corn tissue and found that 6-19% of the Zn remained linked to the macromolecules while the remainder was found in the protopectin and hemicellulose fractions of the roots, grains, and leaves, but not in the cellulose residues. These results suggested that Zn may play a part in the formation or plasticity of the cell wall.

Zinc has also been reported to be involved in protein synthesis and carbohydrate transformations (203, 257). Wood and Sibly (288) noted that Zn-deficient oat and tomato plants exhibited proteolysis in the leaves and that addition of Zn activated protein synthesis. Citing other studies, Thorne (246) documented that Zn deficiency in tomato

plants resulted in nitrate accumulation, followed by proteolysis and amino acid and amide accumulations. According to Wood (286), the failure of tryptophan and protein synthesis in Zn-deficient plants probably involved the destruction of pyridoxal phosphate (Vitamin B_6), a coenzyme required for the synthesis of tryptophan from serine and indole. High phosphatase activity in Zn-deficient plants, due to accumulations of inorganic phosphate, could indirectly reduce activities of the glycolytic and Kreb's cycles and result in decreased amino acid synthesis and nitrate reduction.

Zinc has been shown by Quinlan-Watson (182) to increase the activity of the enzyme aldolase which catalyzes an important step in the respiratory breakdown of carbohydrates. According to Thorne (246) previous workers have reported disrupted carbohydrate metabolism in Zn-deficient plants, such as increase in total sugar; absence of starch and accumulation of an abnormal quantity of calcium oxalate, tannins, and fat. These observations may be linked with decreased aldolase activity in Zn-deficient plants.

Carbonic anhyrase, which catalyzes the dehydration of carbonic acid and participates in the elimination and incorporation of carbon dioxide, was the first enzyme for which Zn was established as a metal component (163, 189). Although this enzyme was initially isolated from animal tissue, its presence in leaves of several green plants has been reported (257). The low content of carbon anhydrase in the non-chloroplast fraction of the leaves of Zn-deficient oat plants was deduced by Wood and Sibly (288) to be a result of metabolic blocking of reactions leading to the formation of proteins and not by absence of sufficient Zn to activate an apoenzyme.

The results of many investigations have revealed the diversity of Zn in its metabolic role of the plant. Numerous intermediate products have been found in Zn-deficient plants which have linked Zn with enzymes, auxin, various amino acids and sugars and in turn the essential metabolic processes of photosynthesis and respiration (203, 246). It appears that Zn deficiency does not directly produce a given symptom in a plant but it does disrupt the normal growth processes with the result that certain intermediate organic compounds may accumulate and others become short in supply.

Zinc Deficiency and Toxicity

During the past four decades, a large volume of literature concerned with the visual and cytological symptoms of Zn deficiency and excess in plants has appeared. Many of these reports have been comprehensively reviewed by Thorne (246), Chapman (48), Sparr et al. (226), Boehle and Lindsay (28), and Sprague (227).

A wide variety of plants are susceptible to Zn deficiency, especially fruit crops such as citrus, tung, cherry, apple, and pear. Viets et al. (261) have categorized crops relative to their sensitivity to Zn deficiency. Very sensitive crops which exhibited deficiency symptoms included corn, field beans, lima beans, soybeans, castor beans, flax, and grapes while alfalfa, grain sorghum, red clover, sudangrass, potatoes, tomatoes, onions and sugar beet were listed as mildly sensitive although some deficiency symptoms were observed. Grasses, oats, wheat, barley, rye, peas, carrots, safflower, asparagus, and mustard were considered Zn insensitive since no deficiency symptoms were evident.

Growth characteristics and leaf symptomatology of acute Zn defi-

ciency are dramatically defined with some crops because of combinations of chlorosis, rosetting, dieback, and depressed or abnormal vegetative growth (48, 246). Since Zn is not readily translocated from old to new tissue, deficiency symptoms usually appear on the new growth and involve developmental retardation and chlorophyll shortage. Symptoms common to many crops include: (a) interveinal chlorosis, due to reduction of chloroplasts and starch grains in the leaves, may appear as light green, yellow or white mottles; (b) necrotic tissue in chlorotic areas of leaves; (c) small malformed narrow thickened leaves due to abnormal broadening and division of palisade cells; (d) shortening of stem or stalk internodes resulting in stunted or bushy plant appearance; (e) early loss of foliage as a result of the decline in auxin activity; (f) cessation of meristematic activity in root tips and, in some cases, presence of tumors or hypertrophic tissue (28, 227, 246). Other cyto-logical symptoms of Zn deficiency have been characterized in various crops and may include fat and oil deposits in chloroplast remanents, accumulation of phenolic materials and tannins in leaves, presence of calcium oxalate crystals in leaves and buds which are indicative of disturbed carbon metabolism, and shrunken plastids (227, 246).

Forage grasses in general do not appear to be very sensitive to levels of soil Zn although Zn deficiency symptoms are fairly common in some of the larger leaved members of the grass family such as corn, sudangrass, and certain grain sorghums (246, 261). Zinc-deficient corn plants have been described to exhibit "white bud" appearance of chlorotic whorl of apical leaves, light-yellow streaking or interveinal chlorosis of the older leaves, stunted plants with shortened internodes, delayed silking and tasseling, and decreased number of cobs and kernels (28, 48).

Legumes are generally more sensitive to Zn deficiency than grasses. Viets et al. (261) noted that even the cotyledonary leaves of bean plants grown in Zn-deficient soils were light green in contrast to Zn-fertilized plots. Reported visual symptoms of various Zn-deficient grain and forage legumes include stunted plant growth, yellow and chlorotic interveinal leaf areas, and, with barrel medic, alfalfa, and clovers, bronze- or brown-colored necrotic spots on lower leaves (48, 82, 227).

Williams (282) advocated that even where deficiencies were not severe enough to have caused the appearance of symptoms, yields may be considerably lower than they would be if the deficiency were alleviated. It was conservatively estimated that over 50% reduction in crop yields generally occurred before deficiency symptoms were visible. Such incipient deficiencies may only be identified with tissue and/or soil analysis.

Zinc toxicity has been noted by many investigators, both in the field and under controlled culture conditions (48). Reports have shown that excess Zn interfered with iron metabolism of plants and produced iron chlorosis in plants such as wheat, oats, citrus seedlings, and tomatoes (246).

Content

The absolute or relative content of Zn can usually vary between wide limits, even in apparently healthy plants. According to Chapman (48), Holmes reported in 1944 that plants of different kinds will show Zn contents ranging from 20 to 10,200 ppm of the dry matter (DM). From compiled data, Chapman (48) showed that for a wide variety of plants, deficiency levels were characterized by Zn levels of less than 20 to

25 ppm in the DM. Ample but not excessive values commonly fell in the range of 25 to 150 ppm. Amounts greater than 400 ppm of the DM indicated Zn excess although critical values of Zn toxicity were not stated. Thorne (246) suggested that a plant with leaf Zn content of less than 15 ppm could be suspected of Zn deficiency.

Actual threshold levels of Zn in plants have not been fully established because of insufficient data. This is not surprising as the level at which response may occur varies to some degree even in the same crop variety, depending on other nutritional or environmental factors. From various sources, Williams (282) noted that the normal range of Zn content in the tops or leaves of alfalfa was between 14-89 ppm while Sparr et al. (226) quoted a range of 9-14 ppm for tops. Boawn and Viets (25) found that Zn-deficient alfalfa plants averaged 8 ppm in the tops, and normal plants contained an average of 13.8 ppm. Viets et al. (261) reported that a Zn level of alfalfa leaves below 15 ppm showed Zn deficiency symptoms and yet Lo and Reisenauer (137) obtained top yields with leaf Zn levels of 6 ppm or greater.

The general consensus of opinion, from work conducted in the temperate regions, was that leguminous herbage species contained higher Zn levels than grasses (82, 227, 261, 282). Carroll and Loneragan (45) ascertained from nutrient studies that at higher Zn concentrations (up to 38 ppm Zn in the external solution) grasses had more Zn in roots and tops than legumes. Generalizing, Sauchelli (203) advocated that grasses and legumes have about the same Zn content averaging between 15 to 60 ppm and plants deficient in this element rarely contained less than 10 ppm. The optimum range for various temperate pasture legumes, as compiled by Williams (282), was from 20 to 80 ppm Zn and certain improved pasture grasses ranged from 10-60 ppm Zn in the tops.

Limited data obtained from tropical studies did not reveal any large relative differences in Zn contents between legumes and grasses. Iljin (112) and Blue et al. (23) analyzed the tops of various tropical legumes and grasses for Zn in Venezuela and Panama, respectively. The range of Zn values for some of the more prominent pasture grasses during the vegetative phase of development were 24-38 ppm for jaraguagrass, 34-48 ppm for guineagrass, 41-60 ppm for paragrass, and 50-60 ppm for pangolagrass. Corresponding Zn values for forage legumes were 28-45 ppm for Desmodium sp., 40-80 ppm for Cajanus indicus, 25-44 ppm for tropical kudzu, and 20-40 ppm for Indigofera sp. Iljin (112) also obtained values of 3 ppm Zn for Andropogon rufus (preflowering stage) and 8 ppm Zn for Vigna luteola (flowering stage) but made no mention of possible Zn deficiency symptoms.

Absorption

When an ion reaches the plant root, three events have been suggested as possibly occurring: (a) penetration of the root by passive movement into the free space; (b) adsorption into external or internal root surfaces; and (c) active or metabolic absorption (75). Various hypotheses, models, and pertinent data have been extensively reviewed (35, 66, 75, 132, 135) relative to mineral uptake of plants. Epstein and his co-workers (67, 68, 69, 71) have characterized the process of active or metabolic absorption of ions in excised barley roots and it appears that the "carrier hypothesis" proposed has gained most favor. This mechanism of active transport involving carriers was considered analogous to the mechanism of catalysis mediated by enzymes and has been interpreted in terms of the Michaelis-Menton enzyme kinetic analysis (68, 69). Fried and Broeshart (75) have defined

active absorption or transport as the accumulation of inorganic ions resulting from the ion combining with a carrier, followed by the ion-carrier combination going through a metabolic step requiring energy which results in the ion being deposited in or associated with the internal metabolic system of the plant. The absorption process is assumed to exhibit ion selectivity, involves expenditure of metabolic energy, dependent upon temperature and oxygen supply, and inactivated by metabolic inhibitors (35).

Foliar applied mineral nutrients, though of secondary importance, have been reported to be readily absorbed and translocated to most plant parts (123). Mechanisms of ion uptake by aerial portions of the plant have also been based upon fundamental enzyme kinetics.

Thorne (246) stated that Zn was probably assimilated mainly as the divalent ion, Zn^{++}, with the possibility of some absorption in a monovalent form, such as $ZnCl^+$. Although zincate ions may occur under alkaline conditions, plant uptake of these ions was not considered appreciable.

The concentration of Zn in culture solution usually regarded as adequate for the healthy growth of most plants has been reported within the range of 2 to 20 ppm (46). Certain studies have indicated that Zn was readily absorbed by normally growing cotton plants from nutrient solutions containing as low as 0.001 ppm and 0.1 ppm Zn (246). Carroll and Loneragan (46) revealed that various pasture legumes achieved 50% of their maximum yield at a nutrient solution concentration of 0.006 ppm.

Absorption of ^{65}Zn by excised barley roots was studied by Schmid et al. (205) in experiments conducted at 30C for up to 4 hours. Labelled Zn was absorbed at a constant rate by the roots bathed in 0.3 ppm Zn

nutrient solution. After 4 hours the ^{65}Zn had been concentrated in the tissue to at least 84 times the level of the nutrient solution. Absorption of Zn was shown to be reduced or inhibited by a low temperature of 4.5C, anaerobic conditions, and metabolic inhibitors. Schmid et al. (206) repeated their earlier study but with nutrient solution concentrations of 0.03 to 0.65 ppm Zn. Results demonstrated that total Zn absorbed increased with increasing concentrations of Zn in solution. Carroll and Loneragan (46) substantiated these findings with intact pasture legume plants grown in flowing culture media. They also noticed that plants contained a higher percentage of total Zn in the roots when growth was limited by Zn deficiency than under optimum Zn supply. This may have been due to a greater reduction in yield of tops compared with roots under deficiency conditions rather than to an actual higher content of Zn in the roots.

There are few published data on rates of Zn uptake by plant roots, and even less at solution concentrations below about 0.01 ppm Zn which more closely approach soil solution levels of Zn. In a still culture experiment, as reported by Carroll and Loneragan (46) Zn was supplied at a level of 0.015 ppm and the absorption rate of Zn by alfalfa and clover was observed to decline from 1,000 ug Zn/100 g fresh weight roots/day to less than 10 ug Zn/100 g fresh weight roots/day after 46 days as Zn was removed from the nutrient solution.

The rate of absorption of ions into the roots of a particular plant species is related to the concentration of the ions immediately adjacent to the root, particularly at low concentrations. This concentration near the root surface is dependent partly on the movement of ions towards the root by the processes of mass-flow and diffusion

and partly on root interception (13). In a growth chamber experiment,
Halsted et al. (91) found that the calculated supply of Ca, Sr, Mn,
and Zn to four plant species by root interception plus mass-flow was
highly correlated with their uptake. The correlation observed between
Zn absorption and supply by root interception plus mass-flow was lower
than for the other cations because considerable quantities of Zn also
reached the root by diffusion. Autoradiographs of ^{65}Zn depletion
around wheat roots in a loamy sand were assessed by Wilkinson et al.
(280) to be similar to those shown for ^{32}P by other workers. Zinc
absorption in this case was not observed to be dependent on mass-flow
of solution to the roots since no difference was found in Zn levels
of tops or roots when transpiration ratios were trebled.

Certain ions and compounds have been shown to influence Zn ab-
sorption by plants. Schmid and Hawf (204) concluded from their nutri-
ent solution studies that the general effect of added cations of Cu,
Cd, and Mn on ^{65}Zn uptake and translocation in intact bean plants was
predominantly to inhibit absorption but not internal distribution.
Bowen (30), working with sugarcane leaf tissue, suggested that since
Zn and Cu exhibited mutual competitive action upon the absorption of
the other, the two elements shared the same specific absorption site.
A second independent mechanism, however, was postulated for Mn absorp-
tion.

Contrary to generally accepted criteria of ion absorption into
cells by the metabolic process, Schmid and Hawf (204) reported that Zn
uptake by excised barley roots was only mildly affected by anaerobioses
and metabolic poisons such as carbonyl cyamide phenylhydrazone and
2,4-dinitrophenol (DNP) even though metabolic involvement of Zn uptake

had been demonstrated by reduced Zn absorption with low temperatures. They concluded that Zn uptake was associated with another mechanism which was only indirectly connected with respiratory activity. However Bowen (30) contended that the absorption of Zn by sugarcane leaves was metabolically activated at one site in that Zn uptake was strongly inhibited to varying degrees by metabolic poisons such as DNP, cyanide, arsenate, Amytal, and Nembutal and by the uncoupling of oxidative phophorylation with respiratory substrates such as succinate.

Epstein and Stout (70) reported a linear increase in ^{65}Zn uptake by tomato plants with increasing saturation of ^{65}Zn when adsorbed on bentonite in amounts less than 0.1%. At higher levels, the Zn in solution and Zn contents of roots were negatively related to the degree of Ca saturation. Maximum Zn content in tomato tops occurred between pH 5.0 and 5.6 when the clay was Ca-saturated in the order of 50 to 70%.

Translocation Within Plants

Nutrient ions normally pass through the roots and are translocated to the plant tops either by mass-flow with the transpiration stream or by a process of ion exchange (287). These ions can accumulate in both plant tops and roots although the relationships between accumulation in the roots and translocation to the tops have not been adequately clarified. According to Fried and Broeshart (75), it was generally accepted that ions moved to the shoots primarily in the xylem but it has not been substantiated as to whether the ions were translocated passively through the "free" space system of both roots or shoots or whether a prior carrier-mediated active transport step was necessary.

The translocation of Zn within the plant may be markedly influ-

enced by other ions or compounds. Biddulph (20) found that plants grown in solutions high in P precipitated Zn along the veins. Under high Fe nutrition less Zn was precipitated apparently because the level of soluble P was reduced by precipitation with Fe. When plants were grown in low concentrations of P, Zn was distributed uniformly throughout the leaves and was not concentrated along the veins. Zinc, like Fe and Ca, was not commonly retranslocated from older leaves to younger leaves as the plant grew. Under low P conditions however, Biddulph (20) demonstrated that ^{65}Zn as well as ^{55}Fe were translocated from injected leaves.

Sharma et al. (209) revealed that P applications decreased Zn levels in the tops of corn, rice, and tomato plants but did not affect root Zn contents appreciably. In the presence of P, added Zn increased Zn concentrations in corn roots more than the tops. Most workers have agreed that normal plant metabolism was dependent upon a physiological balance between P and Zn within the plant (24, 41, 65, 149, 177, 178, 210).

Under conditions of low Zn supply, Ozanne (173) reported that the severity of Zn deficiency symptoms were increased when N supply was increased irrespective of the N source used. Nitrogen application decreased Zn content of plant tops. Under low Zn conditions the Zn level of roots was found to be correlated with the percentage protein N. It was interpreted as resulting from the formation of immobile Zn-protein complexes which fixed Zn in the roots under high N and low Zn conditions. The data of Bergh, 1950, as reported by Thorne (246), supported this concept in that 77% of the Zn retained in roots of pea plants was in the soluble residue whereas 60 to 85% of the Zn in the

top parts was soluble in cold water. Diez-Altares and Bornesmisza (57) recovered most of the ^{65}Zn in the soluble-protein fraction of corn seedlings. The highest values corresponded to solubility groups for basic proteins, nucleo enzymes, albumins, and globulins, as well as prolamines and glutamines.

Zinc-deficient tomato plants studied by Gondwe (87) had lower Ca and, to a lesser extent, Mg concentrations in the roots than normal plants. Zinc levels in the shoots however increased, while potassium levels decreased.

Riceman and Jones (190, 191) revealed that Zn distribution in subterranean clover grown in culture solution during the vegetative stages of growth was not affected significantly but during the flowering stage ^{65}Zn accumulated in the inflorescence and seeds, especially at higher levels of ^{65}Zn supply. The maximum ^{65}Zn content in the leaves was reached before maximum dry weight which probably accounted partly for the apparent decrease of Zn concentration in senescent leaves. Riceman and Jones (193) demonstrated that Zn in fully expanded leaves of subterranean clover was largely retained, and it was only when these leaves became prematurely senescent as a result of Zn deficiency that any of this Zn was retranslocated. Other investigations have also indicated this retranslocation of Zn from leaves and stems into seeds of oats (281), subterranean clover (190), and corn (148).

Wood and Sibly (287) advocated that free Zn ions are not commonly present in plant tissue. No Zn was transported from oat leaves, during senescence, to other organs and the Zn present in the inflorescence came directly from roots and the growing substrate. Working with subterranean clover and _Antirrhinum majus_ in nutrient culture studies,

Millikan et al. (156) noticed that [65]Zn recently absorbed by the roots was preferentially routed to the youngest leaves. Zn was immobilized in old and senescent leaves. Limited recirculation of Zn and [65]Zn was however observed in the roots, hypocotyl, and between and within some leaf tissues of the clover plants.

The effect of light on Zn absorption and translocation has also been studied. Ozanne (174) recorded a greater absorption of Zn and root accumulation by subterranean clover under long-day conditions than under short-day. Maximum Zn deficiency symptoms were observed at the same light intensity as that required for maximum photosynthetic activity but this effect was alleviated by higher light intensities.

According to Sudia and Green (238), light seemed to have a profound affect on [65]Zn redistribution in germinating seeds of soybean. Zinc deposited in the seed coat was not available for the metabolism of the growing seed but light enhanced the translocation of over 50% of the Zn found in the cotyledon, mainly into the epicotyl and leaves of the seedling. This phenomenon may be associated with the role of Zn in the synthesis of tryptophan and auxin which are active in epicotyl and leaves of growing seedlings.

Although Zn can be precipitated, fixed or inhibited in plant tissue by possibly P, various protein materials and other cations, in general Zn seems to move with ease from roots to leaves once absorption has been accomplished; however, its retranslocation from leaves appears to be limited or slow.

Distribution Within Plants

Micronutrients are not generally considered relatively mobile within the plant. Even if an element is completely mobile and can be

translocated to wherever it may be required, its distribution in various parts of a plant is not usually uniform (282). On a dry matter basis the roots and leaves, the young and actively growing parts of a plant, would frequently have the highest concentration of Zn (57). However, if the Zn became deficient while the plant was still growing, the youngest parts would frequently contain less Zn than older ones. This means that the total plant analysis, including plant parts of all ages, may indicate adequate levels of Zn while analysis of young growing parts only would suggest deficiency levels. Zinc content of leaves of known age have provided a reasonably sound basis for evaluating Zn status of growing plants (48, 190).

Riceman and Jones (194) determined that recently absorbed ^{65}Zn in normal subterranean clover plants reached high concentrations in the roots and main axis and rarely moved from the youngest to the fully expanded older leaves, while in plants recovering from deficiency it reached high concentrations in all living tissues, including the oldest leaves. The growth of leaves affected by deficiency was not resumed after the entry of Zn into the tissues, and plant recovery depended upon the production of new leaves and their subsequent growth.

Plant analyses have indicated that Zn accumulates in different parts of a plant in the following order, from most to least: root, leaves, stems, and fruits. Thorne and Wiebe (247) reported the study of Bergh who measured ^{65}Zn uptake by Pisum sativum and found after 36 days that 1.04% of the radiozinc had been absorbed and was distributed in the plants as follows: pea, 18%; shell, 15%; flower, 1%; blade, 26%; stem, 11%; and root, 29%.

Kanehiro (124) and Gladstone and Loneragan (82) have recognized

that older and mature plants had lower Zn concentration in their tissue
than younger plants. In flow culture solution studies with subterra-
nean clover, Riceman and Jones (191) showed that the concentration of
Zn in individual leaves followed the same pattern in each leaf, being
highest before leaf emerges, when dry weight was small, and changing
during growth to reach a maximum content shortly before maximum dry
weight was achieved, then falling off rapidly. Highest levels of Zn
were noted in the terminal portions of the main axis, runners and
laterals, young expanding leaves and petioles, in root tips and at
points along the roots, in parts of the inflorescence, and in the
mature seed of subterranean clover. The same authors (192) have
observed greater Zn levels in nodal tissue, a meristematically active
zone, than in the internodes of clover. Stukenholtz (237) obtained
7 to 10 times the concentration of Zn in the nodes of corn than either
the leaves or internodes.

Roots of deficient plants have shown greater Zn contents than
tops (45, 173, 190, 191, 192, 287). Carroll and Loneragan (45) sub-
stantiated that the Zn levels of roots and tops of various legume and
grass species were approximately equivalent at low Zn concentrations
in the culture solution but with Zn concentrations approaching optimum
levels, the root:top Zn ratio was less than 1.0. However, at luxury
or toxic Zn-nutrient solution levels, root:top Zn ratios were about 2
for subterranean clover and 9 for alfalfa.

Genetic Variants and Plant Nutrition

Quite large differences have sometimes been found in the Zn con-
tents of different but related species, and even between varieties of
the same species. Baker et al. (11) produced evidence that Zn and

other cations as well as ionic ratios, such as P:Zn, were under partial genetic control. Brown (38) reported an instance when of 14 plant species or varieties grown on a Zn-deficient calcareous soil, 7 developed Zn deficiency symptoms, 2 developed Fe deficiency, and 5 had no mineral deficiency symptoms at all. He concluded that genetic variants in plants affected uptake and utilization of a nutrient element by roots.

Brown (38) documented that plant species have been observed to differ in their response to phosphate in accordance with their susceptibility to Zn deficiency. This suggested that plant species under Zn stress differed in their phosphate metabolism or in their ability to absorb Zn. If phosphate accentuates Zn deficiency without interfering in Zn uptake then plant genotypes under a Zn stress must differ in the way they utilize phosphate. Polson and Adams (181) have substantiated Brown's theory in their study of differential P:Zn response of bean varieties to applied Zn. The degree and pattern of Zn deficiency symptoms and P:Zn relations were noticed by Halim et al. (90) to vary with several strains of corn.

Vose (264) has reviewed the varietal differences in plant nutrition and has grouped the determining causes into four general categories: (a) root morphology; (b) exchange-absorption; (c) translocation; and (d) metabolism. Each process was responsible for intraspecific variation in mineral content.

Certain plants take up Zn in quantities far above the average quantity for 'normal' plants. Rice (189) and Chapman (48), in review articles, have quoted values from various sources of 714 ppm Zn in Diodella, 585 ppm Zn in foxtail grown on a sandy soil in which corn

was Zn-deficient, 3,800 ppm in ragweed grown on a Zn mineral outcrop, and 1,540 to 2,000 ppm in tobacco plants growing in a galvanized container.

Zinc in Ruminant Nutrition

Ultimately, the purpose of quality herbage production is for livestock consumption and the production of milk, meat, and wool. Since plant species have been shown to differ in their capacity to absorb Zn from the soil and accumulate the element in their tops, the significance of plant nutrition, soil adaptation, and management in their influence on Zn uptake by the grazing animal is obvious. Mineral interrelationship studies which involve the soil-plant-animal trinity have been emphasized by Ammerman (5).

The production of uncomplicated Zn deficiency in experimental animals and the discovery of Zn in purified enzymes and hormones have given unequivocated proof of the essentiality of Zn in many animals (189). Although extensive areas of Zn-deficient soils were revealed in different parts of the world, only a few cases of overt Zn deficiency have been reported for grazing livestock (254). Legg and Sears (134), however, have observed typical manifestations of Zn deficiency in calves, yearlings, and adult cows under certain range conditions in British Guiana.

Zinc has been reported by Underwood (254) to be a constituent of enzymes (such as carbonic anhydrase, alkaline phosphotase, alcohol dehydrogenase, and glutamic and lactic dehydrogenases) and of tissue. Some values for Zn content in bovine are: liver, 162-208 ppm; kidney, 102-124 ppm; heart, 94-127 ppm; spleen, 100-160 ppm; muscle, 160-430

ppm; bone, 106-155 ppm; and milk, 3-5 ppm (23, 254). The skin and hair have been known to be high in Zn relative to softer tissues.

Under ordinary circumstances Zn is poorly absorbed from the intestinal tract although an increase in the dietary level may be reflected by additional absorption. High levels of dietary Zn are readily excreted (189). Excretion of Zn is mainly by way of the feces although certain conditions of nephrosis and albuminuria may increase levels of Zn excreted in the urine. High levels of Ca, Cu, presence of phytic acid or phytates, and fats and oils have been observed to inhibit Zn absorption. Phosphorus enhanced Zn utilization by an indirect relationship with Ca (254).

Underwood (254) reported the requirement of Zn by cattle to vary between 30-40 ppm when the ration contained 0.3% Ca, with an increase of 16 ppm Zn for each additional 0.1% Ca. Less than 20 ppm Zn in the diet could aggravate Zn deficiency. Zinc deficiency may cause parakeratosis in calves. Symptoms include rough scaly skin, increase in thickness of horny layer of the skin, loss of hair, fading of the coat and breaks in skin and hooves, and swelling of hocks and knees. Symptoms of debilitation are also apparent. Zinc is generally considered nontoxic to animals.

Supplementary Zn sources in feed or in applied fertilizers could help prevent or alleviate Zn deficiency in cattle. Grazing management can affect Zn content of pastures; probably by changing the leaf-stem ratio and the relative proportions of young and old leaf material available for grazing (282).

Hyparrhenia rufa (Nees) Stapf

Hyparrhenia rufa (Nees) Stapf, a tropical grass, has been known as jaragua grass or jaraguagrass in parts of Africa, Caribbean Islands, Central America and South America (6, 9, 98, 127, 142, 168, 231, 278). Various local names for H. rufa include baragua in Cuba, canophora in Puerto Rico (98), faragua or puntero in El Salvador (111), pasto yaragua in Venezuela and Colombia (74, 202) and pasto roxo, sape giantee, capim jaragua, capim vermelho or capim provisori in Brazil (89, 202).

Indigenous to the Old World, jaraguagrass has been highly regarded in the natural grazing lands of many parts of tropical Africa (31, 138, 142, 201, 275, 277). It was considered one of the most economically important pasture species in Uganda (31) and Nigeria (142). Kemp et al. (127) found jaraguagrass to be of sufficient promise in British Honduras to be advocated as a general purpose, economically established, range/ fattening and drought-resistant grass.

Jaraguagrass is becoming an increasingly popular introduction for up-grading native grazing lands or for improved perennial fattening pastures in the Central and South Americas. Its documented attributes include resistance to drought (127, 142, 199), adaptability to diverse climatic and soil conditions (31, 40, 73, 98, 111, 127), ability to compete and smother weeds (199), tolerance to overgrazing (31), resistance to burning (40, 89), ease of propagation (111, 127) and spread (73, 111), palatability (31), and remaining green during the dry season (40). Given optimum conditions of management, jaraguagrass is comparable in quality and productivity to many of the introduced tropical forage grasses. However, there are also reports that if jaraguagrass is overgrazed the pastures become susceptible to weed competition (183, 263, 278), that

quality is poor during the flowering period when hard woody culms are produced (89, 278) and during the dry season when the grass is fibrous, unpalatable, and low in total and digestible crude protein (22, 73, 263), and that the grass is not frost resistant (278).

Whyte et al. (278) considered that jaraguagrass was the most wide-spread pasture grass in tropical Central and South America. It was deemed one of the most promising introduced pasture grasses for cattle production in Panama (141, 168), El Salvador (73), and British Honduras (127). Buller (40) reported that jaraguagrass was cultivated for cutting in the dry tropics of Mexico where Panicum maximum failed. Quinn et al. (183) claimed that jaraguagrass was the most widely grown perennial pasture grass in the livestock area of central Brazil and that it accounted for 65 percent of the country's beef production. Pardi (176), however, estimated that only 33 percent of the animals of central Brazil grazed jaraguagrass pastures but ranked it comparable to P. maximum. Roseveare (199) documented the importance of jaraguagrass in improved natural pastures for the semi-arid regions of central and northeastern Brazil and for the hot savannas such as the Colombian llanos.

Distribution

The natural distribution of the genus Hyparrhenia includes most of tropical Africa (93, 142, 187, 277) where it thrives in natural grassland communities or with woodland type of vegetation (258). Whyte and Rattray (277) recorded 16 main grass associations in Africa and 100 sub-associations according to type of vegetation. The genus Hyparrhenia was found to be dominant in 30 of the sub-associations. Rattray (187) reported that the genus Hyparrhenia was the major component in the

savannas of 43 African territories including Congo, Ghana, Kenya,
Nigeria, Nyasaland, North and South Rhodesia, Sudan, Tanganyika, and
Uganda.

 H. rufa has been introduced and commercially established frequently
as one of the more successful species, in the following countries:
Mexico (40, 44), British Honduras (127, 240), Guatemala (240), Honduras
(9, 102, 196), Nicaragua (242), El Salvador (73, 111, 270), Costa Rica
(6, 22, 202, 243), Panama (141, 168), Colombia (53, 199), Venezuela
(74, 98), Brazil (89, 98, 176, 183, 199, 202), Peru (162), Surinam
(231), Cuba (98), Puerto Rico, Leeward and Windward Islands (98, 231),
Hawaii (275), and Australia (283).

Description of the Specie

 Hyparrhenia rufa (Nees) Stapf (tribe Andropogoneae, Gramineae)
was described as a specie in 1918 (98). In 1829 the grass was botani-
cally known as Trachypogon rufus Nees, in 1830 as Andropogon rufus
Kunth and in 1899 as Cymbopogon rufus Rendle.

 Jaraguagrass is a tall, erect and densely tufted perennial. It is
described in several Floras and in some detail by Hitchcock (98) and
Kemp et al. (127). The leaves are about 2.5 cm broad and 50 cm long
forming tussocks when uncut or ungrazed (278). Erect cylindrical culms
emerge from the tufts of leaves to a height of approximately 3 meters
at flowering time (November-December in Central America). During growth,
the internodes of the culm (7-12 cm in length) are whitish in color and
half-enclosed by leaf sheaths giving the culm a banded appearance (127).
The inflorescence is about 20 to 30 cm long with pairs of racemes borne
towards the ends of numerous branches on long slender flexuous peduncles.
Each reddish-brown raceme is about 2 cm long and bears five to seven

fertile spiklets. The spiklets are flattened from the back, pubescent
with dark red hairs on the pedicels and rachis-joints, and are about
3 to 4 mm long. Each floret has a long (15-20 mm) flexuous awn, twice
geniculate, twisted, reddish-brown and hispidulous (98). Seeds ripen
from the base of the panicle upwards and are generally hand-harvested
when glumes are dark brown. According to Williams (283), seed produc-
tion is low but Whyte et al. (278) quoted a value of 200 kg of seeds
per hectare. Maximum seed germination was observed in British Honduras
(127) to be only 25% in December, 10% in May (planting time) and prac-
tically nil 10 months from harvest. Grossman et al. (89) claimed that
seed germination increased after the jaraguagrass stubble was burned.

Kemp et al. (127) noticed, in British Honduras, that if a culm
was cut, a second culm grew and bore seed but the culm was shorter
and contained less viable seeds. Continuous cutting resulted in per-
sistent culm growth and seed production until the onset of rains.

Environment

By virtue of its distribution throughout the tropical regions of
Africa and Americas and its susceptibility to frost (278), jaraguagrass
is considered a tropical grass. Crowder (53), however, recommended
that jaraguagrass and other specific tropical grasses could be sown in
50 percent of the grazing lands within the temperate zone of Colombia
although these grasses were generally grown in the "climata caliente."
While most investigators have emphasized the drought-resistant attribute
of jaraguagrass and its establishment in drier regions (31, 40, 53, 263,
278), the grass is not so restricted. Indeed, reports (89, 278) in-
dicate that jaraguagrass thrives in heavy rainfall areas subjected to
waterlogging or temporary flooding. Williams (283) regarded jaragua-
grass as suitable for the sub-humid to humid regions of Australia.

Indications are that jaraguagrass is adapted or occurs naturally on most soils, from the infertile and acid red latosols (Oxisols), grumusols (Vertisols), ando soils (Inceptisols), calcimorphic soils (Mollisols), to fertile alluvial soils (Entisols) (78, 231, 258, 278).

The author has observed jaraguagrass growing on both flat and steep topographies. The elevation range of the grass has been noted from sea-level to about 1,000 m (73, 138).

Establishment

Jaraguagrass is established either from seed or vegetatively by division of rootstocks (142, 278). In general jaraguagrass propagated from seed gives more rapid establishment and earlier grazing than rootstocks. Vegetative propagation has been successful in small-plot studies but not under field conditions (127).

Mechanical methods of establishment initially involve seedbed preparation during the dry season in Central America (53, 127). The land, if under natural vegetation, is ideally cleared, bushed, windrowed, stumped, levelled, burned and disc-plowed. The seedbed should, prior to sowing, have a medium to fine tilth and be weed free. Seeds are broadcast mechanically (spinner-type) at a rate of 15-20 kg/ha and covered lightly with a harrow (127, 278). The long twisted awns of jaraguagrass seeds assist in burying the seeds but make spreading difficult. A diluent, such as sawdust, is generally mixed with the seeds to obtain a more uniform distribution. Kemp et al. (127) reported that it was possible to sow 10-12 hectares per day mechanically. Management subsequent to sowing involves allowing the grass to establish seed before cutting or grazing, followed by heavy grazing to aid seed dispersal, and cutting the regrowth for in situ foggage and mulch during

the dry season. Grazing may commence when seedlings are 20-30 cm tall
after onset of the rainy season.

Hand-establishment or the "milpa" practice of Latin America in-
volves underbushing, felling of large trees and burning debris in order
to prepare a rough seedbed (53, 127). Seeds are broadcast by hand be-
fore the rainy season at a rate of about 10-15 kg/ha. In the milpa
system, jaraguagrass is usually undersown with a companion cash-crop
such as corn (127). After the corn is removed, the stubble is grazed
and the grass is allowed to set seed; an essential practice because
of poor seed germination of jaraguagrass. Logs, stumps, and weeds
are burned every year during the latter part of the dry season.

Sowing by hand to complete establishment of jaraguagrass is slow;
usually 24-30 months compared with 14-16 months by mechanical means
(53, 127).

<u>Jaraguagrass/legume mixtures</u>

Jaraguagrass has been grown as a mixture with various legumes in
several countries both in trials and on field scale. The legumes were
expected to increase dry matter (DM) yield, fix atmospheric nitrogen,
and, probably more important, raise crude protein (CP) yield, digest-
ibility, and content in the forage, especially during the dry season
when CP in <u>H</u>. <u>rufa</u> often falls below subsistence level.

In Trinidad (231), jaraguagrass has been grown with <u>Dolichos
lablab</u> and creeping indigo (<u>Indigofera endecaphylla</u>) in mixtures, in
British Honduras with tropical kudzu (<u>Pueraria phaseoloides</u>) and centro
(<u>Centrosema pubescens</u>) and in Panama with indigenous <u>Desmodium</u> sp.

In N. Rhodesia, Smith (220) introduced uninoculated stylo
(<u>Stylosanthes guayanensis</u>) and glycine (<u>Glycine javanica</u>) by oversowing

into an undisturbed <u>Hyparrhenia</u>-dominant veld. Superphosphate was added at a rate of 200 lb/acre. <u>Hyparrhenia</u> veld alone yielded 2,090 lb DM/acre of herbage, 85 lb CP/acre, and 25 lb digestible CP/acre, respectively. The veld and glycine also gave higher yield values than the veld alone. Cattle-grazing trials in Uganda (233) revealed that the greatest value of jaraguagrass and stylo or centro mixtures was during the dry season when liveweight gains of the animals were 63.5 percent greater than those grazing on grass alone. The difference was only 10 percent greater in the rainy season. Centro, filling the bottom of the sward and climbing up the culms, seemed compatible growing with <u>H</u>. <u>rufa</u>. Stobbs and Joblin (236) recorded liveweight gains of over 300 lb/acre/year from animals grazing centro/jaraguagrass mixtures.

Horrell and Newhouse (106) found in Uganda that a S, P, and K fertilized mixture of stylo and centro with <u>H</u>. <u>rufa</u>, <u>P</u>. <u>maximum</u>, and <u>Chloris</u> <u>gayana</u> increased DM yield and CP content of the forage. In the same trial it was shown that unfertilized legume/grass pasture yielded equivalent to grass and 150 lb N/acre but produced 33 percent less DM and 57 percent less CP than a legume/grass mixture with 207 lb P_2O_5/acre. The contribution of N to the pasture per acre per year was 0, 56, 75 and 144 lb N for grass alone, grass and 150 lb N, unfertilized legume/grass sward and fertilized legume/grass mixture, respectively.

Plant Nutrition Studies

Nitrogen

Nitrogen is probably the most important fertilizer element for the nutrition of most tropical grasses. Published investigations generally indicate positive response of grasses to applied nitrogenous

fertilizers, especially under favorable conditions of rainfall and with adequate soil P, K, and Ca supplies. This is not surprising since most of the trials are conducted on soils inherently low in nitrogen and other available plant nutrients.

Linear yield responses by jaraguagrass to increasing rates of N were observed in trials in the Pacific Region of Costa Rica (6). The average DM yields from 0, 88, and 176 lb N/ha applications after 33 days were 1.2, 2.2 and 3.7 tons/ha, respectively and after 51 days were 3.3, 4.7 and 5.9 tons/ha, respectively. Kemp, et al. (127) found that 21 lb N/acre increased DM yield, over control plots of jaragua-grass by 300 percent and CP by one percent. Blue (22), conducting trials in Costa Rica, also showed positive responses by jaraguagrass to increasing rates of N fertilizer. Application of 140 kg N/ha, for example, produced 29,930 lbs DM, 311 lb N, and 1,944 total CP/ha and 6.5% CP compared to control values of 18,550 lb DM, 156 lb N and 977 total CP/ha and 5.2% CP. Positive responses were also obtained from applications of P but not from K. Smith (217), studying the effect of broadcasting 47 lb N/acre/year on a Hyparrhenia veld in N. Rhodesia, found that the forage yields increased to 7,420 lb DM/acre in the first year and to 12,031 lb DM/acre in the second year. Average CP percentages and total CP were 9.3% and 688 lb/acre for the first year and 7.8% and 224 lb/acre for the second year, respectively. In a later trial, Smith (221) revealed that nitrogen applications to Hyparrhenia veld up to 189 lb N/acre gave a positive linear forage yield response up to 6,100 lb DM/acre/year with an average CP analysis of 9.1%, 31% crude fiber (CF), 47% digestible CF, and 557 lb CP/acre/year.

Tergas (243) measured the yield of jaraguagrass at various intervals

during the dry season in Costa Rica after applying 0, 75, and 150 kg
N/ha and a basic dressing of 37.5 kg P/ha. After 48 days, the DM
yield per hectare of the forage for the control and 150 kg N/ha treat-
ment was 1,381 kg and 3,638 kg, respectively. Root yields were 2,176
kg and 3,082 kg for the same treatments. After 143 days, the forage
yields were 2,276 kg and 4,981 kg and root yields were 4,659 kg and
3,583 kg DM/ha for the control and 150 kg N/ha treatments, respectively.
Average CP percentages after 48 and 143 days were 5.06 and 1.33 without
N, 6.27 and 1.37 with 75 kg N/ha and 9.00 and 1.85 with 150 kg N/ha,
respectively. Nitrogen also increased the N content of roots, cellu-
lose concentration of the forage from 30 to 38% at the end of the
experiment and increased in-vitro cellulose digestion from 44% to 49%
after 43 days.

Martin and Skyring (144) remarked that recoveries of fertilizer
N by growing crops seldom exceed 50% and following crops, grown in the
same soil, do not generally utilize more than an additional 10%. Smith
(217, 221) revealed that N recoveries from two separate trials involving
Hyparrhenia veld were 40 and 35%, respectively. Blue (22) found that
the average N recoveries from applications of 70, 140, and 210 kg N/ha
to jaraguagrass were 33.6, 50.2 and 40.6%, respectively. Tergas (243)
determined that N recovery from jaraguagrass was less than 45% from
the first harvest to less than 10% at the end of the experiment irre-
spective of the N treatment. A range of 15-153% N recovery was reported
by Noland et al. (168) from western Panama jaraguagrass pastures; the
high values were postulated to be from additional N in the urine and
feces of grazing heifers. Blue (22) noted abnormally low total N
contents in jaraguagrass herbage during the dry season in Costa Rica

and hypothesized that N was probably translocated from the shoots to
the grass roots as the dry season progressed. He also observed that,
at the same N equivalent, urea, sodium nitrate and ammonium nitrate
sources of N did not show any significant differences in their effect
on jaraguagrass (forage and protein yields/ha or CP %).

Complete Fertilizers

Individual plant nutrient studies, other than with N, have rarely
been investigated using jaraguagrass. However, plant nutrients in
combination usually produce higher forage yield and quality which are
just as spectacular and consistent as with N alone. Noland et al.
(168) showed in western Panama that application of six rates of a
10:30:10 complete fertilizer mixture increased jaraguagrass DM and
total protein yields and total animal gains of grazing heifers. Appli-
cation of 2,000 lb/ha of the complete fertilizer produced 30,472 lb
DM/ha and 2,840 lb total protein/ha of jaraguagrass and 740 lb/ha of
total liveweight gain while the unfertilized plots produced only
17,910 lb DM/ha, 1,182 lb total protein/ha of forage and 165 lb/ha
total liveweight gain. They calculated that DM and CP increased linearly
up to 40 and 80 lb N/ha and that 1 lb N was equivalent to 8 lb CP in the
herbage and 2 1/2 - 3 lb liveweight gain by growing heifers. Awan (9)
fertilized a 10-year-old jaraguagrass pasture with four rates of N
(up to 120 kg N/ha of urea) and two rates of P and K (0 and 80 kg/ha
of P and K as superphosphate and KCl, respectively) and recorded in-
creases in DM yield of herbage from 2,120 to a high of 5,790 kg/ha with
N alone and 5,230 to a high of 9,140 kg/ha when N, P, and K were applied
together. The addition of 4 tons/ha of dolomitic limestone, 90 kg N/ha,
100 kg P_2O_5/ha, 100 kg K_2O/ha, and trace elements to a jaraguagrass

pasture in central Brazil (179) resulted in an average annual yield
of 7,074 kg DM of herbage/ha and 668 kg CP/ha. Without complete fer-
tilizer the pasture only yielded 2,786 kg DM of herbage and 211 kg
CP/ha/annum. Blue (22) and Brockington (34) also demonstrated that
value of complete fertilizer dressings on _Hyparrhenia_ dominated pas-
tures in Costa Rica and N. Rhodesia, respectively.

Chemical Composition and Feed Value

Organic and nitrogenous compounds

In jaraguagrass the organic compounds, on a DM basis, usually
vary within the following limits: crude protein (CP) 3 - 12%, ether
extract (EE) 0.5 - 3.0%, crude fiber (CF) 30 - 40%, and nitrogen-free
extract (NFE) 40 - 50% (74, 117, 138, 168).

Crude protein content may vary widely, increasing with increase
in available soil N and decreasing with the age of the plant or its
parts. The effect of applied N fertilizers on forage CP values has
been demonstrated. In Costa Rica, Blue (22) observed that delayed
fertilizer application and harvest resulted in decreased CP content of
jaraguagrass. The CP contents of herbage fertilized early (October 5)
were 6.0% of the DM in 50 days and 2.5% after 110 days. When fertilized
late (October 23) the CP values decreased from initial values of 7.3 -
8.6% to 8.0, 3.0 and 1.5% after 32, 80 and 95 days, respectively. It
was calculated that early fertilizer application caused reduction of
CP by 60% in 50 days and 75% in 123 days while delayed application
caused a 80% reduction of CP in 95 days. As the dry season progressed
Blue (22), in another trial, found a marked decrease in CP values of
the herbage. In December the CP content of jaraguagrass was 3.3% of
the DM, 1.5% in January and 1.4% in March. Kemp et al. (127), working

in British Honduras, established that lengthening the interval between clipping caused a lowering of CP values in jaraguagrass although DM and CP yields per acre increased. Mean CP values were 6.5% of the DM, 5.6% and 4.7% when the herbage was clipped at 4, 7, and 9 week intervals, respectively.

Juko and Bredon (120) studied the chemical composition of leaves and whole plant of six tropical grass, including jaraguagrass, in Uganda. After 6 weeks, it was observed that the variation in percentage of leaves in relation to the whole plant was more influenced by the specie of grass and various climatic conditions than stage of growth. The average percentage of leaves to whole plant was 25% for jaraguagrass compared to 42% for guineagrass and 45% for molassesgrass (_Melinus minutiflora_). They found that CP and EE were consistently higher in leaves. Jaraguagrass recorded the highest CP value in the leaves compared to the whole plant, especially at the end of the dry season. At any stage of growth all the grasses had lower crude fiber values in the leaves relative to the whole plant. Main increases in CF content of the herbage were during the first 6 weeks of growth. Although NFE values varied, they were generally higher in the leaves. In a Brazilian experiment, Lewin and Melotti (136) noticed that the CF content increased and EE and CP decreased during the flowering period of jaraguagrass. Lignin content increased markedly during the same period and continued to increase up to 14.51% of the DM during the dry season.

Minerals

Jaraguagrass DM usually contains 9 - 16% total ash and 2 - 4% silica-free ash. Values for silica-free ash were found by Juko and

Bredon (120) to be higher in the leaves of grasses than in the whole
plant. Typical ranges for plant nutrients in jaraguagrass are as
follows: 0.5 - 1.5% N, 0.1 - 0.3% P, 1 - 2% K, 0.2 - 0.5% Ca, 0.1 -
0.3% Mg, 0.05 - 0.15% Na, 100 - 300 ppm Fe, 35 - 75 ppm Mn, 25 - 40
ppm Sr, 0.02 - 0.06 ppm Co, 20 - 30 ppm Cu, and 25 - 35 ppm Zn (23, 74,
112, 117).

Palatability and intake

Many reports have indicated that jaraguagrass was palatable if
grazed during early stages of growth but with maturity, especially
during flowering and dry periods, the grass became very coarse, fibrous,
low in nutritive value and unpalatable (22, 73, 89, 127, 142, 263, 278).
Grossman et al. (89) noticed in Brazil that jaraguagrass lost its nu-
tritive value and palatability if grazed below a height of 30 cm.
Bredon and Horrell (31) maintained that jaraguagrass grown in Uganda
was highly palatable to livestock despite its habit of producing many
hard woody culms. The culms were generally ignored by the cattle in
favor of the more palatable leaves. Also in Uganda, Juko and Bredon
(120) revealed that the ratio of leaves to whole plant in a number of
tropical grasses, including jaraguagrass, increased up to 6 weeks of
growth and declined slightly for the remaining 10 weeks. The lowest
ratio was recorded during the time of full seed development after which
the ratio increased.

Milford and Minson (151) in Australia ascertained that a marked
decline in intake occurred when the CP content of herbage fell below
the 7% value. Since during the dry season many tropical grasses,
especially jaraguagrass, have CP contents below the threshold value,
the importance of legumes, supplementary nitrogenous feed or continuous

grazing of larger pasture areas have been advocated to ensure adequate forage intake.

Digestibility

Kemp (127) surmized that jaraguagrass was highly digestible. Carrera (44) analyzed a number of tropical grasses including jaraguagrass, guineagrass, and elephantgrass and found, on a DM basis, that the total digestible nutrients (TDN) were 16.2, 1.2 and 12.13% and digestible crude protein (DCP) was 1.6, 0.8, and 0.9% for the grasses, respectively. From in-vitro cellulose digestion studies on jaraguagrass, Tergas (243) concluded that herbage maturity was accompanied by decrease in digestibility of the forage. The values were still considered as fairly good during the dry season.

Digestible crude protein was found to be generally higher in leaves as compared to the whole plant. Juko and Bredon (120) also observed that DCP usually decreased with maturity of the forage especially during the first 4 months. They quoted a threshold value of 2% DCP of the DM as being the minimum for maintenance level of cattle. It was noted that at the end of the dry season the DCP values for jaraguagrass were 0.32% of the DM in the whole plant and 1.97% in the leaves. Blue (22) noticed that the digestibility of protein in jaraguagrass decreased from 40 - 50% during the flowering period to 5 - 15% during the dry season.

Investigations into the degree of herbage selection by grazing cattle were made by Hardison et al. (92). They concluded that grazing cattle showed an instinctive preference for the leafy portion of the grass over stems and leafy herbage at an immature stage. Cattle consumed, by grazing, a diet 23% more CP, 37.3% more fat, 25.6% more ash and 16.8%

less CF than the composition of clipped samples. These and other
observations (120, 235) explained the survival of local cattle in
areas where jaraguagrass was one of the predominant grasses even though
the chemical composition of whole plants (taken as an indication of
consumed grass) contained sufficient nutrients to meet the require-
ments of the cattle only when the forage was in its youthful stage of
growth (120). If selectivity is true, then the difference between
the chemical composition of stems and leaves would be an important con-
sideration and the chemical composition of the whole plant, as clipped
for analysis, would be insufficient as a criterion for the economic
value of a grass.

Performance under cutting and grazing

Frequent cutting (or grazing), as with other grass species, re-
duces the DM yield of jaraguagrass, but herbage quality is higher than
when cut (or grazed) only once or twice a year. However, Noland et al.
(168) found in western Panama that an average fertilized plot of jara-
guagrass gave 9,682 lb/ha more DM and 1,324 lb/ha more protein when
grazed and clipped three times than plots clipped once after 6 months.
Kemp et al. (127) recorded, on fertilized jaraguagrass pastures, that
yield increases of 10,900 lb, 16,700 lb, to 16,400 lb DM/acre/year
with longer cutting intervals from 4, 7, to 9 weeks, respectively.
Mean CP contents however decreased from 6.5, 5.6, to 4.7% of the DM
for the same clipping intervals. Under $3-$, $6-$ and 9-week cutting regimes,
Crowder (53) measured DM production of jaraguagrass to be 13.5, 44.1,
and 56.7 short tons/ha, respectively. At the end of a 6-week cutting
interval, lush, leafy grass had accumulated to a height of 75 cm or
more and contained up to 16% CP of the DM. With a 9-week cutting in-

terval the stems had elongated and formed seed heads. Similar obser-
vations were made by Watkins and Lewy-van Severen (270).

Continuous clipping to a height of 2 inches resulted in a 7% de-
crease in DM per acre per year compared to a clipping height of 5
inches. But Kemp et al. (127) did not find the differences in clipping
height statistically significant. Watkins and Lewy-van Severen (270)
examined cutting heights of 4, 8, and 12 inches and found that jaragua-
grass produced the highest fresh weight when cut at 4 inches. At a
3-month cutting interval and 4-inch cutting height, they recorded an
average yield of 28,140 lb DM/acre and 1,100 lb CP/acre and a CP value
of 3.9%.

Whyte et al. (278) recommended that stock should be turned onto
jaraguagrass pastures before growth exceeded 40 to 50 cm, at which
stage the herbage may be closely grazed. In order to maintain the
grass in good condition of vigor and productivity, Grossman et al. (89)
advocated rotational grazing of the pastures. Although Bredon and
Horrell (31) noted that jaraguagrass withstood overgrazing, the grass
would not persist under continuous close grazing (142, 278). Stobbs
(234) observed that jaraguagrass developed a more prostrate habit of
growth under close grazing.

Pasture evaluation studies in Uganda indicated that the intensity
of stocking was the most important factor influencing animal productiv-
ity (234). It was essential that stocking rate be adjusted according
to the dry and rainy seasons. During the rainy season (June to October)
and under fertile soils, jaraguagrass pastures in British Honduras (127)
supported one breeding cow per acre but during the dry season (April to
May) and flowering period, the pasture supported only one cow per 2 acres.

Stobbs (234) maintained that heavy stocking rate (0.5 acre/head/cattle) with concurrent low availability of pasture and less opportunity for grazing give significantly higher output of liveweight gains per acre but lower individual animal production. The mean liveweight gain per acre per year for cattle grazing a jaraguagrass and stylo mixture was 377 lb for a stocking rate of 0.5 acre/head and 147 lb for 1.5 acre/head. He also noticed that the lower stocking rates of 1.0 to 1.5 acre/head preserved a higher percentage of planted species (70% jaraguagrass, 20% stylo, and 10% miscellaneous species) while the highest stocking intensity of 0.5 acre/head reduced the jaraguagrass stand (26% jaraguagrass, 20% stylo and 54% other species). In Colombia, Ramirez et al. (184) calculated the average liveweight gain of bullocks grazing continuously on jaraguagrass pastures to be 0.38 kg/head/day at a stocking rate of 1.0 ha/animal and 0.29 kg/head/day at at stocking intensity of 0.5 ha/animal. They recommended the optimum stocking rate of 0.67 ha/animal weighing about 300 kg.

Animal Production

Reports in the literature of direct productivity measurements in terms of liveweight gains or milk yields are scanty for jaraguagrass, and often referring to relatively short periods of utilization or mixed swards.

The popularity of jaraguagrass in Brazil for fattening cattle has been mentioned (43, 89, 176, 183). The number of cattle grazing jaraguagrass in central Brazil was quoted by Pardi (176) in 1966 to be 1,410,251 with an average cold dead weight of 249.1 kg/head and a killing out value of 57.3%. Guineagrass, the second most important pasture specie, supported 912,307 head of cattle with an average of 240.0 kg/head

and 57.4 killing out percentage. Carneiro et al. (43) found the average liveweight gain of 140 Guzerat cattle, grazing jaraguagrass pastures for over 4 years, to be 23.7 kg/head during the 84-day dry season (with limited supplemental feed) and 88.8 kg/head during the 168-day rainy season. Over a period of 3 years in Mexico, Carrera (44) reported the mean liveweight gains of cattle grazing jaraguagrass, guineagrass, and pangolagrass to be 0.25, 0.53, and 0.55 kg/animal/day, respectively. Average production of beef recorded for the three grasses were 196, 175, and 353 kg/ha/annum, respectively. Also in Mexico, Teunissen et al. (245) found similar results.

Beef production from Uganda pastures was studied by Stobbs (233) using East African Zebu cattle. Over a 3-year period, jaraguagrass-centro mixed swards averaged 14.3% increase in liveweight gain over the grass alone. This increase was especially significant in the dry season when the mixture produced liveweight gains over 160% of the cattle grazing jaraguagrass alone. He also found the liveweight gain of cattle grazing pure stylo, jaraguagrass and centro, and guineagrass to be 834, 970, and 903 lb/acre/annum, respectively.

Fertilizer application can be expected to influence stocking rates and liveweight gains through its effect on herbage production and quality. Quinn et al. (183) investigated beef production from Zebu steers grazing six tropical grasses, including jaraguagrass, guineagrass, and pangolagrass. Each plot was given a basic fertilizer application of 100 kg N/ha and 75 kg P_2O_5/ha after which the treatments on the split-plots were control (no further fertilizer applications) and 100 N (3 applications of 100 kg N/ha and one application of 100 kg P_2O_5/ha over a period of 3 years). Jaraguagrass, guineagrass, and pangolagrass

recorded the highest daily animal gains, beef production/ha, and provided the greatest number of steer days/ha. No significant difference was found between the control and 100 N treatments in daily animal gains. The average daily gains for cattle grazing jaraguagrass were 0.49 and 0.48 kg/animal/day for the control and 100 N treatments, respectively. Greater amounts of beef production were recorded by cattle grazing the 100 N treatment. For example, the average yearly beef production from jaraguagrass and guineagrass was 235 and 205 kg liveweight/ha for the control pastures and 320 and 330 kg/ha for the 100 N treatment, respectively. Higher average rates of stocking were generally obtained from 100 N plots. The number of steer days/ha/annum was 453 and 607 on control and 589 and 766 on 100 N treatments for jaraguagrass and pangolagrass, respectively. Jaraguagrass was noted to always have sufficient forage for grazing.

<u>Conservation</u>

Conservation of jaraguagrass in the form of hay or silage has been reported in Brazil, El Salvador, Costa Rica, British Honduras and N. Rhodesia (22, 89, 127, 199, 218, 263). Whyte <u>et al</u>. (278) recommended that jaraguagrass should be cut for hay or silage before flowering at a height of 60 - 70 cm and that 4 to 5 cuts during the growing season were feasible.

Smith (218) revealed that mature <u>Hyparrhenia</u> veld in N. Rhodesia, whether cut for hay or left as "standing hay" or foggage, was a stemmy, low quality forage deficient in protein. Analysis of the leaves and stems gave CP values of 2.9% and 1.9% and CF values of 31.3 and 42.9%, respectively. Voluntary intake of veld hay was low with heifers but with nitrogenous supplement in the diet (urea or groundnut meal) the

daily intake of hay increased by 140% with concomitant increase in liveweight gains. In a later trial, Smith (219) studied the apparent digestibility of mature _Hyparrhenia_ veld hay during the dry season by feeding the hay _ad lib_ to indigenous Zebu cattle. Mature veld, harvested at the end of the rains as hay or green forage, contained 50% digestible organic matter (DOM), 3.0% CP and 0.6 digestible CP. By mid-dry season in July, the DOM progressively decreased to 38% and the digestible CP was negligible. Voluntary intake of the forage decreased from approximately 12 lb DM/1,000 lb animal/day at the end of the rains to 8 lb DM in mid-season. The seasonal decreases in digestibility values were accentuated by reductions in DM intake so that a diet of mature veld herbage in mid-dry season was grossly deficient in both energy and protein. Again supplementary protein and urea were beneficial in correcting the dietary protein deficiency and, in turn, the energy deficiency by increase forage intake.

Blue (22) described a method of conservation practiced in Costa Rica which he referred to as "deferred grazing." Jaraguagrass was allowed to grow during part of the rainy season and was saved in the field for grazing. This method is similar to the "standing hay" or foggage practice described by Smith (218, 219).

Pests

Other than weed infestations, reports in the literature on pests of jaraguagrass were not found. The author has observed mild attacks of armyworms (_Laphygma_ sp.) in transplanted jaraguagrass in Panama.

Gramineaceous and woody broadleaf weeds have caused rapid deterioration of overgrazed and poorly managed jaraguagrass pastures in countries where the grass has been an introduced specie. Bernal _et al_.

(19) in Colombia and Swezey and Montano (241) in Central America found
that Tordon (picloram) with 2,4-D and 2,4,5-T herbicides gave accept-
able brush and herbaceous broadleaf weed control on rangelands in which
H. rufa was dominant. In western Panama, for example, the fresh weight
of jaraguagrass was 6.7 - 6.8 tons/acre for the herbicide-treated plots
and 2.5 tons/acre for the control after 100 days. After 10 months the
yields were 4.0 tons and 2.3 tons/acre, respectively (241).

Indigofera hirsuta Linn.

Introduction and Distribution

Indigofera hirsuta L., widely known as hairy indigo, is a legume
native to tropical Asia, Australia and Africa (104). The first record
of its introduction to the New World was by USDA in 1908 and later in
1914 and 1916 (197). There were no further reports until 1931 when
some small plants were found growing at the Florida Agricultural Exper-
iment Station. Since then hairy indigo has attracted attention as a
possible summer crop in citrus groves and fields of Florida. Seed was
offered commercially in Florida in 1945 (104). It has been cultivated
as a cover crop, for green manure, forage crop, silage, and hay (6, 22,
99, 169, 197, 269, 276).

Hairy indigo has been recorded as introduced or a constituent of
the pasture system in the following countries: Indonesia, Ceylon, S.
Rhodesia (276), Zambia (259), southeastern USA (99, 104, 169, 197, 269,
276) Costa Rica (22, 231), Guadeloupe, Barbados (231), Venezuela (112),
and Argentina (158).

Description of the Specie

Indigofera genus (tribe Galegeae, Leguminosae) comprises 300 species

found in all tropical regions and as far south as the Cape in Africa (276). The specie, *I. hirsuta* is an erect-prostrate, annual which grows into a shrubby type of plant (197, 276). The legume produces heavy foliage on medium to fine stems which become woody as the plant approaches maturity. Leaves are compound-pinnate with short bristle-like hairs covering the leaflets. Stems may attain a height of 4 - 7 feet (12 - 20 dm) and the whole plant may have a diameter of 5 - 7 feet (15 - 20 dm) (269). Salmon- (269), purple- or rose-colored (276) flowers are arranged in dense, elongated racemes. Cylindrical pods develop and hang from the racemes at maturity. The seeds are crowded into these bivalved pods causing them to develop into cubes resembling very small dice. Averaging 200,000 to a pound, the seeds are considered small. Some 30 - 60% of the seeds do not germinate after falling to the ground in autumn. In Florida, this ensures a good volunteer crop during the following spring (269).

An early-maturing variety was obtained in 1943 with substantial seed producing potential and adaptability to the long growing season of central and south Florida (197). Hollowell et al. (104) recognized two strains of hairy indigo in cultivation. A large late-maturing strain, maturing in November, produced more forage than the early strain and was adapted to the southern half of Florida. The smaller early-maturing strain produced seeds 3 to 4 weeks earlier than the late strain and was grown as far north as Georgia. Hodges (99) claimed that other species of *Indigofera* do not compare with the early- and late-maturing strains of *I. hirsuta* in general value.

Whyte et al. (276) and Verboom (259) reported shrubby perennial types of hairy indigo which exhibited creeping habits were slow in growth, poor in seed production and generally unpalatable to livestock.

Environment

Adapted to the tropical areas of the world, hairy indigo is sensitive to the cold and killed by first frosts (197).

Ritchey (197) advocated that hairy indigo was adapted to a wide range of soils but thrived in the sandy soils of Florida. The consensus of a number of workers indicated that the legume was generally grown on well-drained, moderately acidic, sandy soils (99, 104, 269, 276). Hairy indigo was also noted to tolerate wide fertility and soil moisture regimes (99), especially dry conditions (269, 276).

Establishment

Under Florida conditions, Ritchey (197) recommended sowing hairy indigo in early spring or the middle of March to May. The risk of poor growth and seed production was greater with delayed planting. He suggested that seeds should be sown to a depth less than an inch at a rate of 3 - 5 lb/acre if drilled, or 6 - 10 lb/acre if broadcast. Lower seeding rates were better for seed production and higher rates for forage, green manure or cover crop. Wallace (269) advised the use of the cultipacker with seeding attachment for planting. A good stand of hairy indigo may be obtained by discing an old pasture of the legume in May or June. Hairy indigo could be sown with corn and other spring crops just before the last cultivation but because of shading effect, may require 3 - 4 weeks to establish and gain vigor. Interplanting of the legume in permanent pasture soil and allowing it to reseed every year was also advocated.

Unless the area had been previously seeded with hairy indigo, inoculation of the seeds with rhizobia of the cowpea cross-inoculation group was recommended (3).

Hairy Indigo and Grass Mixtures

Although hairy indigo may be compatible with a wide range of tropical grasses, published reports of its use in pasture mixtures are rare. In Florida, Kirk et al. (129) reported a cattle-grazing study in which hairy indigo was grown in mixture with pensacola bahiagrass (Paspalum notatum). Moffat (158) documented the use of hairy indigo with pangolagrass and Paspalum rojasi in a sub-tropical region of Argentina.

Plant Nutrition Studies

One of the criteria of merit in a pasture species is an ability to respond to increases in soil fertility. Although hairy indigo tolerates acid, sandy, and infertile soils, it will respond to improved fertilizer or fertility regimes. Ritchey (197) noted on poor soils in Florida that hairy indigo responded to 1,000 lb/acre of lime on acid soils and 300 - 500 lb/acre fertilizer of a mixture, such as 0-10-10 or 0-14-10, applied prior to sowing. Wallace (269) suggested that no fertilizer was required for hairy indigo on fertile crop land, if grown after fertilized row crops. He recommended a 300 lb/ha application of 0-12-12 fertilizer mixture on poor Florida soils at seeding. As with most legumes, one would speculate that adequate levels of P, K, Ca, Mg, Fe, Mo, and other trace elements would enhance the quality and produc-tivity of hairy indigo.

Chemical Composition and Nutritive Value
Crude protein and fiber

Wallace (269) stated that the desirability of hairy indigo as a livestock feed was enhanced by its high crude protein content. Values for the CP contents of hairy indigo were reported to be 22.6% CP of the

DM at the 6-inch stage of growth, 21.9% at the 12-inch stage, 15.8% at prebloom, and 13.6% at late bloom. Norris and Lawrence (169) presented analytical data for hairy indigo at the early bud stage of growth. The CP contents of the tender tops, leaves (same plant), and whole plant were 20.71, 20.93, and 10.82% of the DM, respectively, while the CF values were 10.53, 8.85, and 32.80% of the DM, respectively. These figures are indicative of the qualitative value of hairy indigo in a grazing system, especially during periods (for example, August to October in Florida) when the forage grasses have low CP and high CF values and, in turn, low nutritive values.

Minerals

The paucity of analytical data on hairy indigo makes it difficult to present optimum ranges of elemental concentrations in the plant. Only specific values can be reported.

Norris and Lawrence (169) documented the total ash contents of the leaves and whole hairy indigo plant to be 6.09 and 3.86% of the DM, respectively. Typical elemental contents in hairy indigo from various sources were 0.56 - 2.61% P, 0.25 - 0.63% K, 1.79 - 2.75% Ca, 0.33 - 0.56% Mg, 47 ppm Fe, 58 ppm Mn, 40 ppm Zn, 27 ppm B, 27 ppm Cu, and 1.7 ppm Mo (112, 169, 269).

Palatability

According to Wallace (269), cattle did not generally graze hairy indigo readily if other forages were available but once the taste was acquired they seem to like it. Hodges (99) claimed the legume lacked palatability but Blue (22) expressed an opinion to the contrary.

Performance Under Cutting and Grazing

If hairy indigo was cut or grazed before stems became woody, new growth would appear and a second or third grazing would be feasible (197). Wallace (269) recommended that the legume should be grazed or cut when it had grown to a height of 15 - 18 inches and while still in the vegetative stage. Rotational grazing should be practiced to prevent excessively defoliated legume. Grazing intensity must be reduced prior to flowering if seed is required for a volunteer crop.

Conservation

The conservation of hairy indigo as high quality hay has been recorded by Wallace (269), Whyte et al. (276) and Hollowell et al. (104) in Florida and by Blue (22) in Costa Rica. In Florida, the legume is cut 6 inches from the ground for hay when the crop is 15 - 18 inches high. The first harvest is usually made in late July or early August after which a second cut may be made if seed production is not desired. Hay produced in Costa Rica (22) was estimated to have a CP content of 20% of the DM, appeared palatable and was deemed an important supplementary forage.

Wing and Becker (284) investigated the intake of cows from silages made from four legumes, including hairy indigo, and four grasses in Florida. Hairy indigo, without an additive, produced silage with 24.2% DM, 56.6% DM digestibility, 56.1% TDN and 2.6% digestible CP on a DM basis. This product provided cows with slightly above maintenance requirement for energy but below maintenance for protein which was obviously not well preserved. The cows only consumed 64.5 lb of silage per 1,000 lb liveweight which was well above maintenance requirement. Moderate amounts of protein concentrate were still recommended for lactating cows.

Hairy Indigo as a Cover Crop

Hairy indigo is regarded as a good green manure or cover crop in Florida because it furnishes abundant organic matter and nitrogen, exhibits rapid growth and spread, and moderates the soil temperature by shading (104, 164, 269). Wallace (269) reported that hairy indigo usually produced an average of 7 to 10 tons/acre of green crop residue which contained between 90 to 130 lb N/acre. Yields of over 20 tons/acre of green material with over 200 lb N/acre have been recorded.

Symbiosis with Rhizobium

Like most legumes of the Papilionateae sub-family, hairy indigo produces root nodules in symbiotic relation with a strain of bacteria (Rhizobium japonicum) belonging to the cowpea cross-inoculation group (3, 171).

Norris and Lawrence (169) reported that Dr. G. D. Thornton prepared a number of Rhizobium cultures for hairy indigo used in a series of demonstrations in Lake and Indian River counties of Florida. No noticeable differences between inoculated seed and control plots were observed, presumably because the appropriate Rhizobium strain was present in the soil of the check plots.

Toxicity and Lameness in Cattle

There have been reports in the past of toxicity in cattle grazing Indigofera species. A hepatotoxin, DL-indospicine (3-nitropropionic acid) has been isolated from a specie related to hairy indigo, namely creeping indigo (Indigofera endecaphylla) in Australia (7, 94, 110). Zoebisch et al. (291) utilized a bioassay technique with chicks to diagnose legume toxicity. Ground leaf meal of 10 strains of hairy indigo

fed to day-old chicks for 21 days revealed that, while growth was depressed, no toxic symptoms were recognized. Research has yet to confirm the presence of toxic compounds in hairy indigo.

Cattle grazing a dense growth of indigo, usually during the summer rainy season, have been observed to develop an irritation and swelling of the skin above the hooves. This was later accompanied by severe lameness (99). Wallace (269) attributed this malady to the hairs of the legume penetrating the wet skin of grazing cattle. Hairy indigo grown in mixture with a grass did not cause any such symptoms in cattle.

Diseases and Pests

Ritchey (197) and Wallace (269) advocated that hairy indigo was generally free from disease and insect injuries and resistant to the root-knot nematode (Meloidogyne sp.). Good et al. (88) considered hairy indigo as a nematode-reducing crop.

Norris and Lawrence (169) have noted that hairy indigo was a host to the burrowing nematode in Florida and was attacked, as transient host, by armyworms. The author has observed cucumber beetles of the genus Diabrotica attacking seedlings of the legume in eastern Panama.

MATERIALS AND METHODS

Two pot experiments were established, under semi-natural environmental conditions to study the effect of Zn uptake by jaraguagrass (H. rufa) and hairy indigo (I. hirsuta). Field experiments were also conducted on established jaraguagrass pastures.

Location of Experiments

Pot Experiments

An open and level site about 8 m x 18 m was selected, near the University of Florida's Field Laboratory at Santa Fe O.C.I.S.[1] Base Camp, Darien Province, eastern Panama, for the pot studies and enclosed with a 2 m-high barbed-wire fence. Four slatted-wooden benches, 1.0 m wide, 0.7 m high, and 7.7 m long, were constructed to accommodate the pots.

Field Experiments

Two field experiments (Fig. 3) were established at each of the following locations: (a) Santa Fe -- "La Mereda" ranch owned by Sr. A. Pretto about 800 m from the Santa Fe O.I.C.S. Camp (latitude 9° 3' N and longitude 78° 9' W); (b) Patino -- Hammac-Banz Ranch (latitude 8° 15' N and longitude 78° 15' W); and (c) Yaviza -- Quintero Ranch about 1.5 km up Rio Chico from Yaviza (latitude 8° 9' N and longitude 77°

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[1] Office of Interoceanic Canal Studies.

40' W). The sites selected represented some of the major soil groups encountered in the Darien Province particularly suitable for pasture production. It was fortunate that established jaraguagrass pastures existed in these locations and that the respective owners gave permission for experimental use.

Soil Profile Description

Soil profile pits were excavated to varying depths in unfertilized jaraguagrass pastures at Santa Fe, Patino, and Yaviza to aid soil characterization at the respective experimental locations. Morphological descriptions were made for each genetic horizon in accordance with the methods outlined in the Soil Survey Manual (224). Depth, Munsell color notation, texture, consistence at time of sampling, structure, boundary and thickness of horizons, presence of mottles, and other pertinent characteristics were recorded. Bulk samples were obtained from each genetic horizon and placed in labelled plastic bags. After air-drying at the Field Laboratory the samples were sealed in plastic bags for shipment to Gainesville, Florida. A rapid colorimetric pH determination (Truog) was made in the field for each horizon using a special three-component indicator and finely ground $BaSO_4$ powder (114).

Four profile pits were dug at the Santa Fe field study site from which soil for the pot experiments was collected. Two soil profile pits were excavated and sampled at each of the Yaviza and Patino locations.

Soil Collection for Pot Studies

Approximately 700 kg of surface (0-15 cm) soil was randomly col-

lected on June 30, 1967, within the characterized area at Santa Fe.
The soil was transported to the Field Laboratory in burlap sacks,
spread on heavy-ply plastic sheets overlying a tarpaulin, and frequently
turned to facilitate air-drying. Roots, rocks, and other extraneous
matter were removed and the soil was passed through a 6-mm^2 plastic-
coated screen. Intermittent turning of the sieved soil continued for
6 days to ensure uniform drying before samples were taken for the pot
studies and chemical analysis.

Procedures for Pot Experiments

Jaraguagrass Experiment
Experimental design

A $3N \times 3P \times 2Ca \times 3Zn$ factorially arranged completely randomized
block design was used for the jaraguagrass Zn uptake pot study. Treat-
ments were replicated three times to ensure adequate estimation of
experimental error under the semi-natural environmental conditions of
this study.

Treatments

Fertilizer treatments were as follows: (a) the equivalent of 0
(N_0), 50 (N_1), and 100 (N_2) kg N/ha in the form of urea (46.6% N);
(b) the equivalent of 0 (P_0), 50 (P_1), and 100 (P_2) kg P/ha as CaH_4
$(PO_4)_2 \cdot H_2O$ (24.6% P); (c) the equivalent of 0 (Ca_0) and 2,000 (Ca_1)
kg Ca/ha from $CaCO_3$ (40% Ca); and (d) the equivalent of 0 (Zn_0), 15
(Zn_1), and 30 (Zn_2) kg Zn/ha applied as $ZnSO_4 \cdot 7H_2O$ (22.7% Zn). An
equivalent basic dressing of 90 kg K/ha was added to all treatments
in the form of K_2SO_4 (44.3% K). Reagent grade chemicals were used.

Establishment and maintenance

Sieved and air-dry Santa Fe soil was weighed to 2,150 g and packed into individual plastic pots after thorough mixing with the specific Ca and P treatments. After sowing with about 50 cleaned jaraguagrass seeds, each treatment received the basic K dressing in solution. Each pot received 400 ml deionized water prior to placement on the experimental benches on July 27, 1967. The grass seeds germinated within 4 days in all pots. Nitrogen treatments were applied in solution one week after germination and after thinning to give four seedlings per pot. On August 21, 1967, the Zn treatments were applied to the soil surface in solution.

Following the first and second harvests, the specific N treatment rates were sprayed on the stubble and soil.

As a preventative measure, periodic sprayings of dieldrin (a chlorinated hydrocarbon insecticide) on all treatments were made at an equivalent rate of about 240 ml/ha to thwart insect infestations on jaraguagrass seedlings. Weed seedlings were pulled from the soil of each pot and allowed to desiccate on the soil surface.

Sampling procedure

Plant samples.--Jaraguagrass forage was harvested three times between September 23-24, November 5-6, and finally December 5-6, 1967. All plants were cut 8 cm above the soil surface using a stainless-steel scalpel. Harvested forage from each treatment was immediately placed into a labelled paper bag, dried in a force-draft oven for 24-36 hours at 70C, and then sealed in a labelled plastic bag for shipment to Gainesville, Florida. Roots were collected after the third (final) forage harvest by carefully emptying the entire contents of each pot

into a large plastic bucket and gently easing and shaking the roots
from the soil. This method minimized root damage and loss. After
careful washing in tap-water followed by rinses in deionized water,
the roots from each pot were placed in labelled paper bags and dried
in the oven at 70C for 48 hours before shipping in sealed plastic
packets to Florida.

Soil samples.--Approximately 300 g of soil were sampled into
labelled plastic bags from each treatment after removal of jaraguagrass
roots and mixing the soil thoroughly. All precautions to minimize
contamination were observed.

Hairy Indigo Experiment

Experimental design

A 3P x 2Ca x 3Zn factorially arranged completely randomized block
design was planned for the hairy indigo Zn uptake pot study. The ex-
periment was replicated three times.

Treatments

Fertilizer treatments were as follows: (a) 0 (P_0), 50 (P_1) and
100 (P_2) kg P/ha equivalent of Ca $H_4(PO_4)_2 \cdot H_2O$; (b) 0 (Ca_0) and 2,000
(Ca_1) kg Ca/ha equivalent as $CaCO_3$; (c) 0 (Zn_0), 15 (Zn_1), and 30 (Zn_2)
kg Zn/ha equivalent in the form of $ZnSO_4 \cdot 7H_2O$.

Each pot also received an equivalent of 90 kg K/ha, applied as
K_2SO_4, as a basic dressing. Reagent grade chemicals were used.

Establishment and maintenance

The specific rates of Ca and P fertilizers, for each treatment,
were thoroughly mixed with 2,150 g of sieved air-dry Santa Fe soil
which was then packed into plastic pots. About 20 hairy indigo seeds
were sown to a depth of 3-5 mm in each pot and lightly covered with

soil. The basic dressing of K was then applied in solution. Each pot received 400 ml of deionized water prior to placement on the experimental benches on July 15, 1967. Germination of seeds began 3 days later. Each pot was thinned after one week to give four seedlings per pot. Additional seeds were sown in each plot as an insurance against possible seedling loss during the establishment period. Thereafter the pots were constantly kept free of weeds which were allowed to desiccate on the soil surface of infested pots. Zinc treatments were applied in solution onto the soil of all pots on August 12, 1967.

Insect pests were kept under control, as for the jaraguagrass pot study, throughout the experimental period using dieldrin.

Pre-experimental plantings of hairy indigo were found to nodulate effectively in Santa Fe soil without previous seed inoculation with the appropriate rhizobia. As a consequence of this finding and the difficulty in trying to import rhizobial inoculant into Panama, the hairy indigo seeds of the pot experiment were not inoculated with rhizobia.

Sampling procedure

Plant samples.--Hairy indigo forage was harvested from each treatment on September 22, November 4, and finally on December 4, 1967. Forage and plant samples were harvested, dried, and handled in the same manner as described for the jaraguagrass pot experiment.

Soil samples.--After the roots were harvested, 300 g of soil were sampled from each pot, air-dried, and sealed in labelled plastic packets for shipment.

Procedure for Field Experiments

Experimental Design

Each field experiment was a 3 + 1 randomized block design repli-

cated three times. Two experiments were established, at Santa Fe,
Fatino, and Yaviza, to study the effect of Zn uptake by jaraguagrass
grown alone and by jaraguagrass/hairy indigo mixed swards.

Treatments

Jaraguagrass field experiment

The four fertilizer treatments for the jaraguagrass field plots
were as follows: Compound fertilizer mixture with 0; 15; and 30 kg
Zn/ha equivalent; and no fertilizer (control). The compound fertilizer
mixture was composed of the equivalent rate of 100 kg N/ha as urea
(46% N), 100 kg P/ha as triple-superphosphate (20.76% P) and, for the
Santa Fe experiment only, 1,000 kg Ca/ha in the form of slaked lime
(42.8% Ca). Zinc was applied as $ZnSO_4 7H_2O$. Each plot received 90 kg
K/ha equivalent from K_2SO_4 (40% K). With the exception of $ZnSO_4 \cdot 7H_2O$,
which was of reagent grade quality, all fertilizer materials used were
of commercial grades.

Slaked lime $(Ca(OH)_2)$ was substituted for $CaCO_3$ as the Ca source
because the latter fertilizer material could not be obtained in Panama
in time for establishment of the field trials. Insufficient quantity
and the phytotoxic nature of slaked lime resulted in the Ca treatments
being restricted to the Santa Fe field studies and the rate being re-
duced from 2,000 to 1,000 kg Ca/ha, respectively.

Mixed sward field experiment

Fertilizer treatments for the jaraguagrass and hairy indigo mixed
sward study were the same as for the jaraguagrass field trial except
the N treatments were omitted as it was assumed that the legume would,
in time, add to the N increment of this sward. Again only the Santa Fe
trial received Ca treatments for reasons previously mentioned.

Establishment and Maintenance

Field experiments were laid down at Santa Fe, Patino, and Yaviza on 3-, 3-, and 2-year-old jaraguagrass pastures, respectively, which had not previously received chemical fertilizers. Topography was gently rolling (Santa Fe and Patino) to flat (Yaviza) with relatively uniform soil conditions. At each location a section about 30 m x 15 m was fenced off from the rest of the pasture to accommodate both experiments. Jaraguagrass was trimmed to a height of about 10 cm. Excess herbage was raked off so that the individual plots could be staked out.

Each plot measuring 5 m x 2 m (0.001 ha) was established with the long axis adjacent and parallel to the next plot. The two experiments were arranged opposite to each other. Weeds and extraneous matter were removed from all plots before application of the specific treatments.

The mixed sward experiment was sown with hairy indigo seeds at an equivalent rate of 6 kg/ha in four furrows 5-10 mm in depth, 5 mm in length and 40 cm apart in each established jaraguagrass plot. Seeds were covered with soil which was firmly pressed after the seeds were hand-drilled.

With the exception of Zn, which was applied in solution, fertilizer treatments were evenly broadcasted on each plot by hand. After each harvest the compound fertilizer treatment plots of the pure jaraguagrass sward received 100 kg N/ha equivalent.

Dieldrin was sprayed on all plots at the standard rate after treatments were applied.

Experiments were initiated at Santa Fe, Patino, and Yaviza on August 5, 8, and 12, 1967, respectively.

Sampling Procedure

Plant samples

Forage from the first harvest was collected 21 days after the experiments were established at all locations. The second harvest was made 63 and 112 days after the first harvest for the Yaviza and Santa Fe sites, respectively. Forage sampling consisted of clipping the plant material 8 cm above the ground within a randomly positioned square-meter quadrat (0.0001 ha) with stainless-steel shears. Samples were placed in labelled paper bags, dried in a force-draft oven set at 70C for 24-36 hours, weighed accurately, ground, and sealed in plastic bags for shipment to Gainesville, Florida.

Plots and aisles were uniformly trimmed to a height of 8 cm after forage and soil sampling. Excess herbage was removed from the experimental area.

Soil samples

A composite soil sample from 15 cm core borings was made from each harvested plot and placed in labelled plastic bags. Sub-samples were taken for pH determinations while the remainder of the soil sample was allowed to air-dry prior to sealing in plastic bags for shipment.

Laboratory Soil Analyses

Soil Sample Preparation

All soil samples collected from profile pits, pot and field experiments were air-dried, crushed to pass through a 2 mm (9-mesh) stainless-steel sieve and stored in cardboard cartons after thorough mixing.

Particle-Size Distribution

Particle-size distribution was measured according to the hydro-

meter method as reported by Bouyoucos (29) after dispersing a 50 g
sample of air-dry soil in a 5% sodium hexametaphophate solution
(Calgon) for 36 hours.

Soil pH

Soil pH was determined in a 1:2, weight/volume, soil-water suspen-
sion after 12 hours using a Corning Model 12 pH meter equipped with a
glass and calomel reference electrodes. An additional pH reading was
made 1 hour after solid KCl was added and mixed to the soil-water sus-
pension to give a soil-$1\underline{N}$ KCl suspension.

Soil Organic Matter

Soil organic carbon was analyzed in a 0.5 g oven-dried (105C) soil
sample by the chromic and sulfuric acid method of Walkley-Black as
described by Jackson (114). Soil organic matter was calculated from
soil organic carbon by a conversion factor of 1.724.

Total Soil Nitrogen

Five grams of soil, pre-digested for 24 hours in 100 ml conc.
H_2SO_4, was used to determine total soil N according to the macro-
Kjeldahl method documented by Breland (32).

Acid-Fluoride Soluble Soil P

Soil P, extracted from 1 g soil by 7 ml solution of 0.025 $\underline{N}$
HCl/0.03 $\underline{N}$ NH_4F, was analyzed by the chlorostannous and reduced molyb-
dophosphoric blue method as reported by Olsen and Dean (172). A
Bausch and Lomb Spectronic 20 was employed to measure the blue-color
density of each sample using 6,600A incident light. Phosphorus con-
centration in the extracting solution was obtained from a standard curve.

Exchangeable Soil Ca, Zn, Mg, Fe, Cu, Mn, Sr and K

Exchangeable cations were determined by extracting 10 g of soil with 1 $\underline{N}$ NH_4OAc buffered at pH 7 according to the procedure used by Gamble et al. (80). The elements, Ca, Zn, Mg, Fe, Cu, Mn, and Sr, were determined directly from the NH_4OAc leachate using a Perkin-Elmer Model 303 atomic absorption instrument. Soil extracts of the soil profile samples and soil samples from the first harvest of the field experiments were analyzed by the Stewart Laboratories, Knoxville, Tennessee (80). A Beckman atomic absorption instrument was employed to quantitatively detect Ca, Zn, and Mg while a Bausch and Lomb quartz prism instrument was used to determine Fe, Cu, Mn, and Sr by optical emission spectroscopy.

Standards of specific cations, prepared in the same reagent as the soil extract, allowed calibration curves to be drawn from which the elemental concentration of a particular cation was calculated. An air-acetylene reducing flame was used to determine the Ca, Sr, and Mg values read at absorption wavelengths of 4,227A, 4,607A, and 2,852A, respectively. Zinc, Fe, Cu, and Mn were read at wavelengths of 2,139A, 2,483A, 3,247A, and 2,801A, respectively using an oxidizing flame of oxygen and acetylene.

Soil K was determined from the NH_4OAc extraction by the Beckman Du flame spectrophotometer using an oxygen-hydrogen flame and a wavelength of 7,680A.

Laboratory Plant Tissue Analyses

Plant Sample Preparation

Oven-dry (70C) plant tissue samples from each treatment were

weighed to determine dry matter yield and then ground in a Wiley mill
to pass a 0.4 mm stainless-steel screen. Exactly 0.5 g of ground oven-
dry plant material obtained from the pot experiments was ashed in a
muffle-furnace, first at 250C and then overnight at 450C. After cool-
ing, the ash was sequentially dissolved and evaporated in 40% HCl, conc.
HNO_3 and conc. HCl according to the procedure described by Jackson (114).
The soft ash was finally dissolved in 0.1 $\underline{N}$ HCl, filtered into a 50 ml
volumetric flask, and made to volume with 0.1 $\underline{N}$ HCl. A 2 g sample of
oven-dry forage from the field studies was ashed and finally dissolved
in 0.1 $\underline{N}$ HCl to a volume of 50 ml (80).

All elemental determinations, with the exception of N, were made
from the acid solvent.

The filter paper, containing the residue which remained after the
final washes and filtering of each ashed root sample, was dried at 70C
for 24 hours and weighed before and after careful removal of the residue.
This residue was considered to be essentially soil contaminant and was
used to correct for the root weight ashed and elemental concentration
values.

Plant N

Total N determination of plant material followed the standard
macro-Kjeldahl method as reported by Breland (32) using 1 g of oven-
dry plant samples. Crude protein percentage was calculated from per-
cent total N multiplied by 6.25 (114).

Plant P

Analysis of plant P was made from the 0.1 $\underline{N}$ HCl sample by the amino-
naphthol-sulfonic acid reduced molybdophosphoric blue method of Fiske

and Subbarow (49). The blue-color density was colorimetrically determined using a Bausch and Lomb Spectronic 20 at a wavelength of 6,800 A.

Plant K

Potassium was determined from the acid solution by the flame photometric method described for soil K.

Plant Ca, Zn, Mg, Fe, Cu, Mn, and Sr

Concentrations of Ca, Zn, Mg, Fe, Cu, Mn, and Sr in plant tissue samples were determined directly from the acid solvent by atomic absorption spectroscopy using a Perkin-Elmer 303 atomic absorption instrument in the same manner as described for the corresponding soil cations. Forage elemental values obtained from the first harvest of the field experiments were run by the Stewart Laboratories, Knoxville, Tennessee as reported by Gamble et al. (80).

Data Processing and Statistical Analysis

Quantitative data obtained from the pot and field studies were coded and recorded on computer cards. The computer was programmed to conduct analyses of variance on all plant and soil responses measured. In addition, the raw data were reduced by obtaining main and, where pertinent, interaction tables (256). Means were compared using Duncan's new multiple range test as described by Steel and Torrie (230). Unless otherwise stated, significant differences between means were significant at the 5% probability level ($P = 0.05$).

Regression coefficients were calculated for all significant main and interaction treatment effects in order that multiple regression equations could be formulated. If only the interactions between treat-

ments were found statistically significant the appropriate linear or quadratic regression coefficients for the main treatment effects were also calculated for inclusion in the specific equation. Multiple regression (linear) models[1] were developed for the jaraguagrass and hairy indigo pot experiments so that any significant response could be calculated from tabulated regression coefficients for given fertilizer treatment rates. Since harvest was not originally included as an independent variable, regression equations were expressed in terms of the specific response for each harvest.

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[1] Personal communication with Drs. F. G. Martin and J. McClave, Department of Statistics, University of Florida, Gainesville.

RESULTS AND DISCUSSION

Soil Characterization

Morphological descriptions, extract analyses, and characteristics of surface horizons of the soils used for the pot studies and field experiments are presented in Appendix Tables 68, 69 and 70. Chemical, physical, and mineralogical properties of these soils have been described in some detail by other investigators (2, 85, 188, 278).

According to Gamble et al. (80), the Santa Fe, Patino, and Yaviza soils may be classified into the following orders: Ultisols; Oxisols; and Entisols, respectively.

The high clay content of Santa Fe soils clearly reflects derivation from shale parent material. Dark brown to reddish-brown colors predominate in the surface horizons while red, yellow, and brown mottles occur with greater frequency in the subsoil. The latter feature indicates imperfect drainage with a fluctuating water table. Except for the surface horizons, which have ash deposits from previous burnings, these soils are strongly acid to very acid with depth. Organic matter, total N, and extractable cations and P of the surface horizons are higher relative to the mean values reported for A horizons of eastern Darien soils by Gamble et al. (80). This may again be attributed to ash deposits since the extractable basic cations, especially Ca and Mg, decrease markedly with depth. Extractable Zn, Cu, and Fe are uniformly high and generally increase with depth. Gamble et al. (78)

found that the clay fraction of the Santa Fe soil had high CEC, amorphous materials, and specific surface values. Differential thermal, infrared, and X-ray diffraction analyses of these clays revealed the presence of interstratified mixtures of montmorillonite, vermiculite, and illite minerals with small amounts of montmorillonite, vermiculite, halloysite, and quartz (188). Crystallinity of the clay minerals was obscure because of the high degree of interlayering.

Patino soils, overlying basic igneous parent material, are clayey textured. Clay content usually increases with depth. Reddish-brown and yellow colors are characteristic of the lower horizons and the presence of mottles again indicate imperfect drainage with a fluctuating water table. Soil pH decreases from neutrality at the surface horizon to strongly acid at about 70 cm in depth. Organic matter, total N, and extractable P and Mn are relatively high in the surface horizons. The other extractable cations measured were relatively low in value but were uniformly distributed throughout the sampled profile. Extractable P values were low in the sub-surface horizons. Although lower than Santa Fe soils, CEC, surface area, and amorphous clay values were relatively high. Mineralogical analyses of the clay fraction indicated the dominance of 1:1 phyllosilicates which were halloysitic in nature with smaller amounts of interlayered mixtures of montmorillonite and vermiculite, cristobalite, and quartz.

Derived from mixed sediments, the Yaviza soils are characteristically alluvial resulting in relatively uniform texture, soil reaction, and extractable cations throughout the profile. These soils are generally deep, grayish-brown, fine-textured, and neutral in reaction. Organic matter and total N of the surface soil are relatively high.

Extractable P, Ca, Mg, Mn, and Sr are above the mean values for alluvial soils in Panama (80), but K, Zn, Fe, and Cu values are low. The clay minerals of the Yaviza soils also exhibit high CEC, specific surface area, and amorphous clay values but are poorly crystalline. Vermiculite and some interstratified vermiculite and illite were detected.

Chlorite, gibbsite, and allophane were not detected in any of the mineralogical analyses (78, 188). Comparisons between total and extractable elemental concentrations of these soils together with specific availability coefficients of each cation were studied but no consistent relationships were found for P, K, Fe, and Mn (2). Santa Fe soils, however, had higher total P content than the other soil groups while total Fe and Mn were higher in Patino soils. Yaviza soils had higher total contents of Ca, Mg, Na, and K.

In general, the soils selected for this investigation are fine-textured, imperfectly drained, high in organic matter, and inherently well supplied with N, K, Ca, Mg, and Sr. Low extractable P values belie the relatively high total P contents of the soil. Extractable Zn, Cu, and Fe were found to be low although total content of these elements may be high, especially in Santa Fe and Patino soils which are derived from shale and basic igneous parent materials, respectively. The mineralogical nature of the colloidal fraction reveals the tropical nature of these soils which appear to have a large reservoir for retention of soluble cations against leaching (85).

Rainfall Data

Rainfall data were collected from a gauge set in the pot experiment enclosure at Santa Fe. All experiments were conducted during the

wet season when total mean precipitation was approximately 70 mm per week (80). Experimental plants were therefore not subjected to water-stress during the study period.

Format and Conversion Factors

Experimental results are discussed with respect to plant yields, elemental tissue compositions, soil pH, and extractable nutrients. Data from plant tissue analyses are expressed in terms of oven-dry (70C) weight while soil extractable nutrient values are presented on an air-dry basis.

Yields of jaraguagrass or hairy indigo harvested from the pot studies could be expressed in terms of kg/ha by multiplying the yield in g/pot by 544. Similarly, total P or Ca uptake and total Zn uptake could be converted to kg/ha by multiplying the appropriate uptake values by 5.44×10^{-1} and 5.44×10^{-4}, respectively.

Jaraguagrass Pot Experiment

Following the first jaraguagrass forage harvest, two horses entered the experimental enclosure and ate some of the stubble from the first and second replications before being driven away. Damage appeared to be slight and, consequently, the experiment was continued as planned. Data collected from the second harvest were critically examined and, while no overt deviations of treatment effects were detected, interaction values should be interpreted with caution.

Soil contamination of jaraguagrass crown-root systems varied from 1.02 to 27.94% of the oven-dry weight. Elemental concentrations of crown-root systems were corrected for soil contamination but yield and

total elemental uptake values were not. Total nutrient uptake values for crown-root systems have only been included in tables showing main treatment effects since individual means were more variable.

Summaries of F tests from analysis of variance on jaraguagrass and soil data from the pot experiment are given in Appendix Tables 71 and 72, respectively.

Multiple Regression Model and Coefficients

Multiple regression model for jaraguagrass pot experiment is presented in Appendix Table 73 and the corresponding constants and regression coefficients in Appendix Table 74.

Yields

Oven-dry yields of jaraguagrass ranged from 1.27 to 4.02, 0.59 to 8.20, 0.62 to 8.18, and 4.02 to 20.16 g/pot for the first, second, and third forage harvests and crown-root harvest, respectively. Average forage yields were 2.43, 2.58, and 3.62 g/pot (equivalent to 1,320, 1,400, and 1,970 kg/ha) for the three harvests, respectively. Crown-root yields averaged 8.63 g/pot (equivalent to 5,130 kg/ha) which was about 9% higher than total forage yields.

Main treatment effects

Main effects of applied Zn, N, P, and Ca (lime) on yields of jaraguagrass forage and crown-root systems are summarized in Table 3.

Response to Zn.--Zn levels had no significant effect on forage yields although a positive trend was observed for the first harvest. Examination of the regression coefficients (Appendix Table 74) confirmed that Zn had a positive but incipient effect on forage yields. Crown-root yields were significantly higher than control (Zn_0) with the Zn_2 treatment.

Table 3. Main effects of applied Zn, N, P, and Ca on oven-dry yields
of jaraguagrass forage and crown-root systems.

Treatment[1]	Forage harvest			Crowns and roots
	1	2	3	
	------------------- g/pot -----------------------			
Zn_0	2.38 a[2]	2.62 a	3.23 a	9.10 a
Zn_1	2.44 a	2.45 a	3.01 a	9.35 ab
Zn_2	2.48 a	2.67 a	3.31 a	9.88 b
N_0	1.86 a	3.32 a	1.43 a	6.99 a
N_1	2.61 b	4.14 b	4.06 b	11.25 c
N_2	2.83 c	4.43 b	4.05 b	10.09 b
P_0	2.29 a	2.60 a	3.02 a	9.32 a
P_1	2.54 b	2.63 a	3.20 a	9.69 a
P_2	2.47 b	2.52 a	3.32 a	9.32 a
Ca_0	2.09 a	1.81 a	2.23 a	7.60 a
Ca_1	2.77 b	3.35 b	4.14 b	11.29 b

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15 and 30 kg
Zn/ha; N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha; P_0, P_1, and P_2
to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg
Ca/ha, respectively.

[2]Values followed by the same letter in each column of the specific
treatment groups are not significantly different at 0.05 probability
level.

Response to N.--As expected, applied N significantly (P = 0.01) increased yields of forage and crown-root systems over control (N_0) although the N_1 and N_2 treatment responses were not significantly different from each other by the second and third forage harvests (Fig. 4). Nitrogen increased forage yields over control by 40, 33, and 180% for the three forage harvests, respectively. Crown-root yields were between 44 and 62% higher than control when treated with N.

The calculated maximum yield response for N treatment was 126 kg N/ha/harvest for both second and third forage harvests. Since the N_2 treatment rate was equivalent to 100 kg/N/ha harvest, it was assumed that the rate of yield increment from applied N was declining by the last two harvests. A significant depression of crown-root yields was observed from the N_2 treatment in comparison with N_1-treated pots. Nitrogen, as urea, was applied in solution to the soil surface and may have caused root damage upon rapid hydrolysis to the ammonium form.

Response to P.--Only the first forage harvest exhibited a significant (P = 0.01) yield response to P_1 and P_2 treatments over control (P_0). Such a response was expected during the early, active growth and developmental stages of the grass and its root system.

Response to Ca.--Lime dramatically and significantly (P = 0.01) increased jaraguagrass forage and crown-root yields (Fig. 5). Forage yields were higher than control (Ca_0) by 33% for the first harvest and by 85% for subsequent harvests. An increase was recorded for crown-root yields for lime-treated pots. Beneficial effects of lime, both direct and indirect, in increasing plant yields have been well documented.
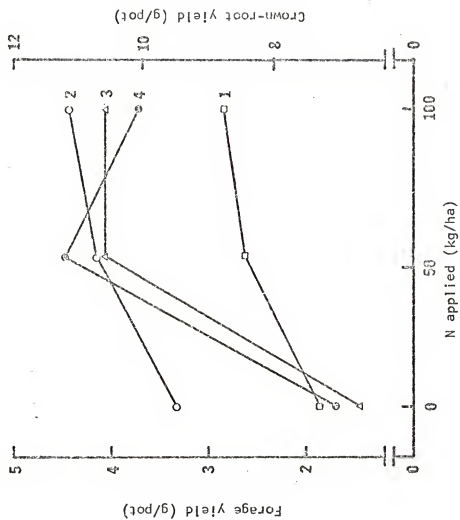
Fig. 4.   Relationship between applied N and oven-dry yields
of jaraguagrass forage and crown-root systems.
(Numbers 1, 2, 3, and 4 refer to first, second,
and third forage harvests and crown-root harvests,
respectively).

Fig. 5. Relationship between applied Ca and oven-dry yields of jaraguagrass forage and crown-root systems.

Not only is Ca an essential plant nutrient, in the form of applied lime in acid soils Ca increases soil pH, availability of most plant nutrients, percent base-saturation, microbiological activity, mineralization of N and organic P, nitrification, and reduces the toxicity of Al, Fe, and Mn and certain organic compounds (227).

Zn x N

The effect of applied Zn and N on yield of jaraguagrass forage and crown-root systems is presented in Table 4. Nitrogen was dominant over Zn treatments in significantly increasing jaraguagrass yields although synergistic effects of Zn were observed for the first forage harvest and crown-root systems (Fig. 6). Under conditions of high N levels relative to Zn there is a possibility that Zn may be rendered immobile in the root by forming a metallo-organic complex with protein (173). A significant but negative N x Zn interaction was observed for the second harvest. Although Zn levels showed a slight enhancement effect on increasing forage yields (Appendix Table 72), application of N seemed to have inhibited yield response to Zn. Nitrogen levels however had a dominant influence on increasing forage yields in general.

The abnormally high crown-root yield recorded for the Zn_2N_1 treatment was primarily due to the N_1Ca_1 treatments which gave yields in three pots of over 19 g/pot.

P x Zn

Applied P and Zn showed little effect on forage and crown-root yields of jaraguagrass (Table 5), although a positive and complementary trend was observed for the first forage harvest with increasing levels of P and Zn.

Table 4. Effect of applied Zn and N on oven-dry yields of jaraguagrass forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		------	------ g/pot	------	------
Zn_0	N_0	1.90 a[2]	2.08 b	1.55 a	6.87 a
	N_1	2.48 b	2.76 c	4.00 b	10.36 b
	N_2	2.75 cd	3.02 c	4.15 b	10.07 b
Zn_1	N_0	1.86 a	1.51 a	1.18 a	6.92 a
	N_1	2.56 bc	2.77 c	3.85 b	11.01 b
	N_2	2.88 d	3.08 c	3.99 b	10.13 b
Zn_2	N_0	1.83 a	2.11 b	1.56 a	7.17 a
	N_1	2.78 d	3.25 c	4.34 b	12.39 c
	N_2	2.85 d	2.65 c	4.02 b	10.07 b

[1] Treatments Zn_0, Zn_1 and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; and N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

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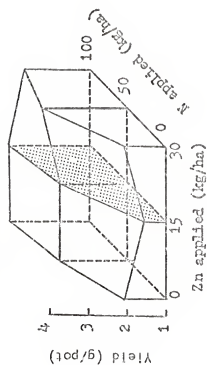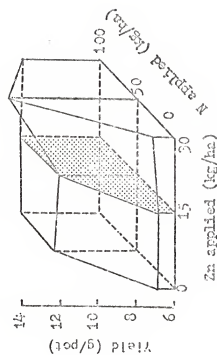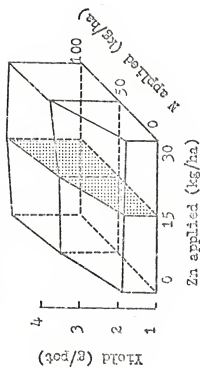
Fig. 6. Relationship between applied Zn and N on oven-dry yields of jaraguagrass forage and crown-root systems.

Table 5. Effect of applied P and Zn on oven-dry yields of jaraguagrass forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		----------------------- g/pot -----------------------			
P_0	Zn_0	2.22 a[2]	2.44 a	3.14 ab	8.79 a
	Zn_1	2.37 abc	2.55 a	2.77 a	9.09 a
	Zn_2	2.27 ab	2.80 a	3.16 ab	10.08 a
P_1	Zn_0	2.42 abc	2.66 a	3.15 ab	9.40 a
	Zn_1	2.54 cd	2.63 a	3.12 ab	9.52 a
	Zn_2	2.65 d	2.59 a	3.34 ab	10.14 a
P_2	Zn_0	2.48 bcd	2.77 a	3.41 b	9.11 a
	Zn_1	2.40 abc	2.18 a	3.14 ab	9.46 a
	Zn_2	2.53 cd	2.63 a	3.42 b	9.41 a

[1]Treatment P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Ca x Zn

The interaction of Ca and Zn applications on jaraguagrass yields
is presented in Table 6. It was evident that lime significantly in-
creased forage yields with each successive harvest irrespective of Zn
treatments. In the absence of lime, Zn_1 and Zn_2 treatments signifi-
cantly increased forage yields over control in the first harvest. A
complementary Zn effect was also observed in the lime-induced increased
crown-root yields.

N x P

Table 7 illustrates the overriding influence of N_i and N_2 treat-
ments in significantly increasing jaraguagrass yields over control.
Phosphorus applications, however, enhanced forage yields from the first
harvest in presence of applied N. A significant increase in yield was
also observed for the N_2P_2 treatment in the third forage harvest.
Both N and P have been reported to stimulate root proliferation (75)
and thus, at high N levels, a complementary effect of P on yield would
be anticipated.

N x Ca

Except for the first forage harvest, interaction of applied N
and Ca on forage and crown-root yields (Table 8) was significant
($P = 0.01$). This implied that differences between yield responses to
N varied with the level of Ca. Lime and N had a complementary effect
of increasing forage yields over control (N_0Ca_0). This effect became
more pronounced with each successive harvest (Fig. 7). Crown-root
yields were similarly increased. The high application of urea (N_2)
after the second harvest may have damaged jaraguagrass roots in unlimed
pots and caused yield reductions of both the crown-root system and

Table 6. Effect of applied Ca and Zn on oven-dry yields of jaragua-grass forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		------------------- g/pot -------------------			
Ca_0	Zn_0	1.97 a[2]	1.82 a	2.40 a	7.54 a
	Zn_1	2.14 b	1.74 a	1.98 a	7.40 a
	Zn_2	2.16 b	1.87 a	2.29 a	7.86 a
Ca_1	Zn_0	2.78 c	3.43 b	4.06 b	10.66 b
	Zn_1	2.73 c	3.16 b	4.04 b	11.30 bc
	Zn_2	2.88 c	3.48 b	4.32 b	11.90 c

[1]Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15 and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 7. Effect of applied N and P on oven-dry yields of jaraguagrass forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		------------------------------- g/pot -------------------------			
N_0	P_0	1.82 a[2]	1.95 a	1.37 a	7.01 a
	P_1	1.91 a	1.97 a	1.48 a	6.89 a
	P_2	1.86 a	1.78 a	1.44 a	7.06 a
N_1	P_0	2.45 b	2.92 b	4.10 bc	11.34 cd
	P_1	2.67 cd	2.99 b	4.01 bc	11.55 d
	P_2	2.70 cd	2.88 b	4.07 bc	10.87 bcd
N_2	P_0	2.59 bc	2.92 b	3.59 b	9.61 b
	P_1	3.03 e	2.93 b	4.11 bc	10.62 bcd
	P_2	2.85 de	2.91 b	4.45 c	10.04 bc

[1] Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha; and P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 8. Effect of applied N and Ca on oven-dry yields of jaraguagrass
          forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		---------------------- g/pot ----------------------			
N_0	Ca_0	1.48 a[2]	1.43 a	1.16 a	6.85 a
	Ca_1	2.25 b	2.37 c	1.71 b	7.13 a
N_1	Ca_0	2.29 b	2.13 bc	3.06 d	8.72 b
	Ca_1	2.92 d	3.73 d	5.06 e	13.79 c
N_2	Ca_0	2.51 c	1.87 b	2.46 c	7.23 a
	Ca_1	3.14 e	3.97 d	5.65 f	12.95 c

[1]Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha;
and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.
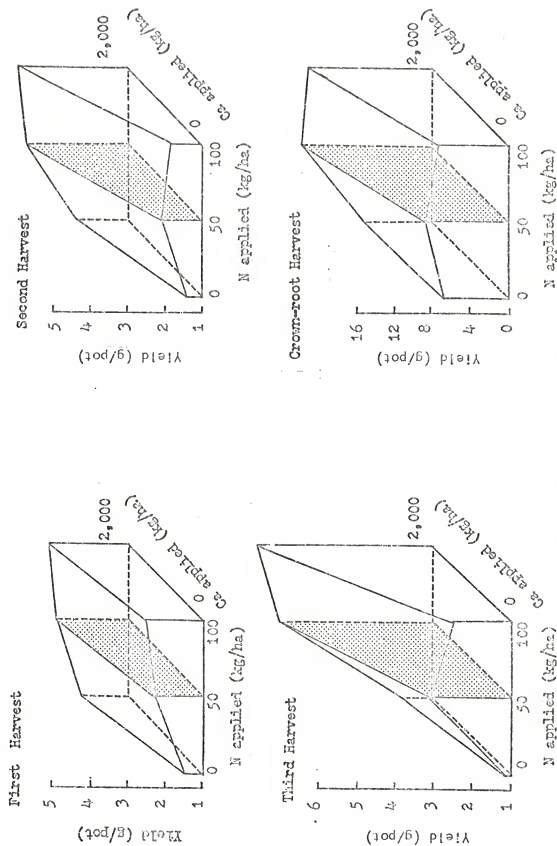
Fig. 7. Relationship between applied N and Ca on oven-dry yields of jaraguagrass forage and crown-root systems.

forage from the third harvest. This could account for the significant depression of yields for N_2Ca_0 treated forage (third harvest) and crown-root systems. When lime was applied, the synergistic effect of the N_2 rate was greater or equivalent to the N_1 treatment in increasing yields.

P x Ca

It is evident from Table 9 that the effect of applied P was negligible after the first harvest as lime was the dominant factor in increasing both jaraguagrass forage and crown-root yields.

Second-order interactions

Second-order interactions of N x P x Ca, N x Ca x Zn, and N x P x Zn were found significant for the three forage harvests, respectively (Appendix Table 71). For the first harvest, it appeared that the effects of N, P, and Ca levels on increasing forage yields differed from each other since no significant first-order interactions were found. In the second harvest, Ca and Zn increased forage yields with varying levels of N, and Ca and N increased forage yields with different levels of Zn but a negative N x Zn interaction was found irrespective of Ca levels. The effect of N x Zn interaction has already been discussed. The N x P x Zn interaction found in the third forage harvest is difficult to explain since neither P nor Zn showed statistically significant effects on yield.

Although measurement of yield response to applied nutrients is of secondary importance in this study, yield of dry matter is a crucial factor in determining total nutrient element uptake by the plant. Multiple regression equations for the relationship between applied nutrients and yields of forage and crown-root systems have not been

Table 9. Effect of applied P and Ca on oven-dry yields of jaraguagrass forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		g/pot			
P_0	Ca_0	1.98 a[2]	1.74 a	2.06 a	7.14 a
	Ca_1	2.60 c	3.45 b	3.98 b	11.15 b
P_1	Ca_0	2.18 b	1.78 a	2.12 a	7.80 a
	Ca_1	2.90 d	3.47 b	4.29 b	11.58 b
P_2	Ca_0	2.13 ab	1.91 a	2.50 a	7.86 a
	Ca_1	2.81 d	3.14 b	4.15 b	10.79 b

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

given in the text primarily because of their length; however, treat-
ment effects on yield response can be readily interpreted by reference
to Appendix Tables 73 and 74.

Lime, mainly through its beneficial effect on ameliorating the
soil environment and general nutrient availability; and N, by encour-
aging vegetative growth, stimulating root proliferating, and regulat-
ing the utilization of other plant nutrients, were responsible for the
significant yield increases by jaraguagrass forage and crown-root
systems. Zinc did have a positive but incipient effect on the yield
responses of forage, and crown-root systems which was partially nulli-
fied by negative N x Zn interactions. Phosphorus significantly in-
creased forage yields in the first harvest and with N had an incipient
but positive N x P interaction for the third harvest. Crown-root
yields were not overly affected by levels of P.

Under controlled environments, increasing the supply of a nutrient
usually results in a decreasing rate of yield response. The first unit
of a deficient nutrient added may result in a very small yield response
but further increments of nutrient will give an increasing rate of
response. An inflection point is finally reached after which the rate
of response passes through a maximum and begins to decrease. A sigmoid-
shaped yield response curve is thus obtained. The inflection point
of maximum rate response is usually at a very low yield level, rarely
exceeding 50% of the maximum yield (75). Calculated inflection points
for yield responses to N and P were over 15% higher than rates used
in this study but Zn in the second harvest was equivalent to the Zn_2
rate of 30 kg Zn/ha. It must be borne in mind that pot studies usually
reflect the quantity of plant-available nutrient in a unit weight of

soil. Plant growth or yield differences, however, may not be due entirely to differences in the ability of a soil to supply nutrients, and may also vary with environmental conditions, such as levels of other nutrients, light intensity, temperature, moisture, and rooting volume.

Zinc Concentration and Total Uptake

Jaraguagrass Zn concentration values ranged from 12 to 45, 21 to 89, 22 to 76, and 51 to 880 ppm Zn for the first, second and third forage harvests and crown-root systems, respectively.

An abnormally high value of 880 ppm Zn was observed for a jaraguagrass crown-root system treated with N_1, P_1, Ca_0, and Zn_2 levels of fertilizers. This value was repeatable upon additional analyses of the original sample. Average forage Zn concentrations were 22, 40, and 43 ppm Zn for the three harvests, respectively, while the crown-root concentrations averaged 157 ppm Zn. Although the first forage harvest value was lower than expected, Zn concentration values were within the range reported by other workers, for jaraguagrass and other pasture grass species (23, 45, 112, 282). Crown-root Zn concentration was almost 4 times higher relative to the forage. This was considered usual by some investigators (45, 247) while others have shown that roots of deficient plants have greater Zn concentrations than tops (173, 190, 191, 192, 287).

Total Zn uptake for the three forage harvests averaged 55, 101 and 137 ug/pot (equivalent to 0.03, 0.05 and 0.08 kg Zn/ha), respectively. In general, both forage Zn concentrations and total Zn uptake increased with each successive harvest but the magnitude was much greater between the first and subsequent harvests. Possible reasons will be mentioned later. High Zn concentrations and yields of the

crown-root systems resulted in the large mean total Zn uptake value
of 1,449 ug/pot (equivalent to 0.75 kg Zn/ha). This was about 5 times
greater than the total mean Zn uptake values from three forage harvests.

Main treatment effects

Main treatment effects on Zn composition of jaraguagrass forage
and crown-root systems are shown in Table 10.

Response to Zn.--Forage and crown-root Zn concentrations were
significantly ($P = 0.01$) and linearly increased by Zn applications
(Fig. 8). Although only the Zn_2 rate gave significantly higher Zn
concentrations in the first harvest, subsequent harvests had higher
forage Zn values with each increment of Zn. The Zn_2 treatment increased
Zn concentrations over control (Zn_0) by 16, 20, and 24% for the three
forage harvests, respectively. Differences between the Zn_2 and Zn_1
treatments and control for crown-root Zn concentrations were more
dramatic, being 64 and 26% higher, respectively. It was interesting
to note that the forage (third harvest) to crown-root ratios for Zn
concentrations were 3.2, 3.5, and 4.2 for the control, Zn_1, and Zn_2
treatments, respectively. The high ratio for the Zn_2 treatment suggests
that Zn was probably accumulating in crown-root systems by the third
forage harvest.

Total Zn uptake by forage was only significantly increased by the
Zn_2 treatment (Fig. 9). This was not surprising since forage yields
from the Zn_1 treatment were generally lower compared to control. Crown-
root systems showed significant response in total Zn uptake with in-
creasing Zn levels. These values were not corrected for soil contamina-
tion but the response was too great to be discounted. Forage Zn con-
centration values were observed to be generally low; averaging 22 ppm.

Table 10. Main effects of applied Zn, N, P, and Ca on Jaraguagrass forage and crown-root systems.

	Concentration				Total uptake			
	Forage harvest			Crowns and roots	Forage harvest			Crowns and roots
Treatment[1]	1	2	3		1	2	3	
	ppm				ug/pot			
Zn_0	21 a[2]	35 a	38 a	121 a	49 a	95 a	126 a	1,026 a
Zn_1	22 a	40 b	43 b	152 b	54 a	96 a	130 a	1,337 b
Zn_2	25 b	43 c	47 c	198 c	61 b	113 b	156 b	1,925 c
N_0	20 a	33 a	36 a	154 a	38 a	61 a	53 a	1,063 a
N_1	22 a	41 b	43 b	149 a	56 b	119 b	175 b	1,670 c
N_2	25 b	44 c	48 c	167 a	70 c	124 b	183 b	1,615 b
P_0	23 a	40 a	43 a	150 a	53 a	100 a	129 a	1,325 a
P_1	22 a	41 a	43 a	162 a	55 a	104 a	139 a	1,554 c
P_2	22 a	39 a	42 a	159 a	56 a	96 a	143 a	1,470 b
Ca_0	23 a	43 b	45 b	174 b	49 a	75 a	104 a	1,353 a
Ca_1	22 a	37 a	40 a	140 a	61 b	127 b	170 b	1,546 b

[1] Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha; P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.
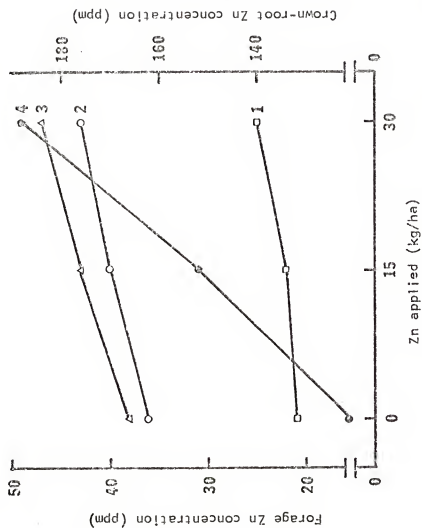
Fig. 8. Relationship between applied Zn and Zn concentrations of jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4, refer to first, second, and third forage harvests and crown-root harvests, respectively).
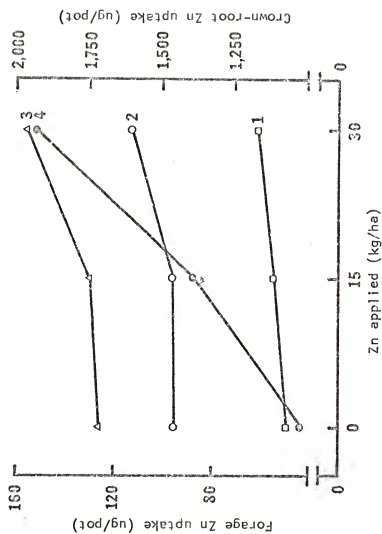
Fig. 9. Relationship between applied Zn and total Zn uptake by jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4, refer to first, second and third forage harvests and crown-root harvests, respectively).

Subsequent harvests showed that mean forage Zn concentrations were
uniformly 15-22 ppm higher. This effect also accounted for the rel-
atively higher total Zn uptake values. The general increase in forage
Zn concentrations by the second harvest could be attributed to: (a)
release of indigenous soil Zn from mineral or organic matter sources
by microbiological activity or by soluble organic complexing agents
which counteract fixation processes; (b) leaching of K (applied in the
form of K_2SO_4 as a basic dressing to all treatments) and the subsequent
acidification effect of the sulfate ion in increasing availability of
soil Zn; or (c) overall development of jaraguagrass and the intensifi-
cation of its root system (12, 143, 161, 166, 203). By the third har-
vest, increase in total Zn uptake was essentially a result of higher
forage yields.

Response to N.--Nitrogen significantly (P = 0.01) increased both
Zn concentrations and total uptake in the forage from all three har-
vests (Figs. 10 and 11). Except for the first forage harvest when
only the N_2 treatment was significantly different from control and N_1,
forage Zn concentrations for N levels were significantly different
from each other. Forage Zn concentrations for the second and third
harvests were 65 to 95% higher than the first harvest. Increasing N
did not significantly increase Zn concentrations of the crown-root
systems.

Total Zn uptake by forage increased significantly over control
with applied N, but the differences between N_1 and N_2 treatments were
not significant for the second and third harvests. This was expected
since forage yields for N_1 and N_2 rates were not significantly dif-
ferent. Since a significant increase in total forage Zn uptake was
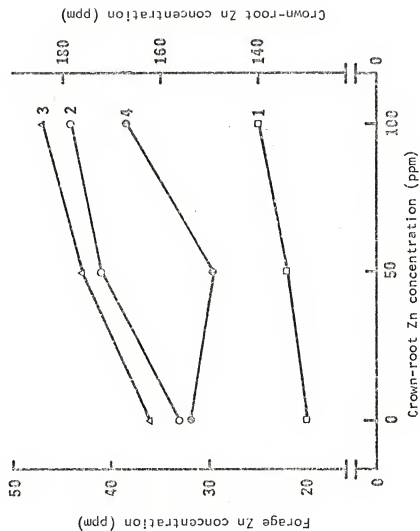
Fig. 10. Relationship between applied N and Zn concentrations of jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4, refer to first, second, and third forage harvests and crown-root harvests, respectively).
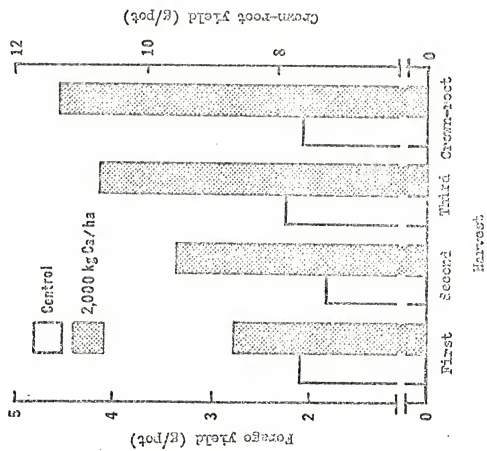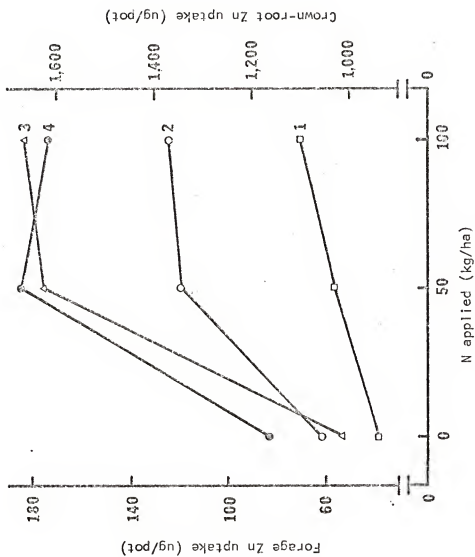
Fig. 11. Relationship between applied N and total Zn uptake by jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4, refer to first, second, and third forage harvests and crown-root harvests, respectively).

observed in the first harvest from N_1 treatment over control, it was evident that the dilution effect of higher forage yields from N_1 treatment resulted in nonsignificant difference in Zn concentration from control. Total Zn uptake by crown-root systems was also significantly responsive to increasing N levels although the lower response value from the N_2 treatment compared to N_1, was partly a reflection of corresponding differences in yields and partly to the abnormally high Zn concentration value reported earlier.

These data are in agreement with numerous reports of increase in Zn availability or plant uptake in response to N fertilizer applications (76, 154, 161, 180, 213, 225, 237). The stimulating effect of N on plant growth and extension of a root system that would tap a wider area probably accounts for observed increases in Zn concentration and total uptake by plant tissues.

Response to P.--No significant Zn concentration or total uptake responses were recorded for jaraguagrass forage to applied P. Although Zn concentrations of the crown-root systems were not significantly affected by P, total Zn uptake values were significantly higher for P_1 and P_2 treatments over control. An abnormally high value of 880 ppm Zn in the crown-roots for a P_1 treatment level resulted in the significant difference between P_1 and P_2 treatments. The higher total Zn uptake in roots relative to tops suggests that, at high P levels, Zn may be immobilized in the crown-root systems.

Several workers have also found that phosphate applications have either no effect or a beneficial one in increasing Zn composition of plants (26, 27, 90, 118, 167, 246, 260).

Response to Ca.--With the exception of the first forage harvest,

lime significantly (P = 0.01) decreased Zn concentration and increased total Zn uptake of jaraguagrass forage and crown-root systems (Figs. 12 and 13). The lower Zn concentrations in plant tissues may be attributed partly to the dilution effect of higher yields from liming and partly to antagonistic lime-Zn interactions in the soil which will be discussed later in more detail. Evidently the effect of lime was negligible on forage Zn concentrations up to the first harvest, despite a significant increase in yields. Higher total Zn uptake by jaraguagrass as a result of liming was essentially due to the effect of lime on increasing plant yields, which masked negative effects of lime on Zn availability in the soil. While liming increased yields over control by 32, 85, 85, and 48% for the three forage harvests and crown-root systems, respectively, total Zn uptake was only increased over control by 24, 70, 63, and 14% for corresponding harvests, respectively. The lower difference between control and lime treatments for the crown-root systems was partly due to an abnormally high value for the control treatment reported earlier.

Zn x N

The effect of applied Zn and N on Zn composition of jaraguagrass is shown in Table 11. A complementary effect of Zn and N treatments on forage and crown-root Zn concentrations was observed, especially for the second and third forage harvests (Fig. 14). In the first harvest only the Zn_2N_2 treatment was significant in raising forage Zn concentration to a mean value of 28 ppm Zn although a positive trend was noticed in forage receiving Zn and N fertilizers. It would appear that the immediate Zn requirement of jaraguagrass was met by the soil prior to first harvest and this, together with relatively small rooting volume
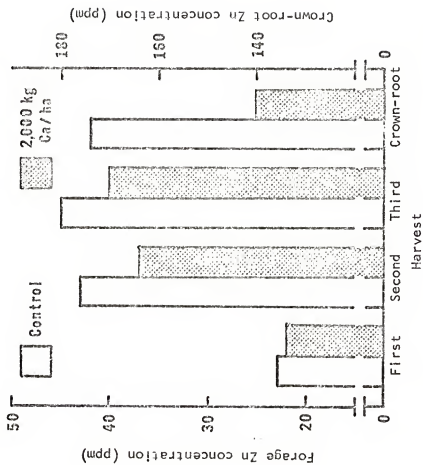
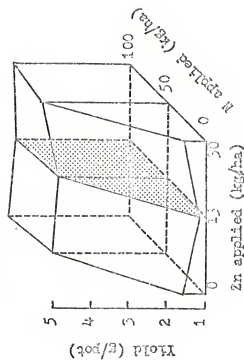Fig. 12. Relationship between applied Ca and Zn concentrations of jaraguagrass forage and crown-root systems.
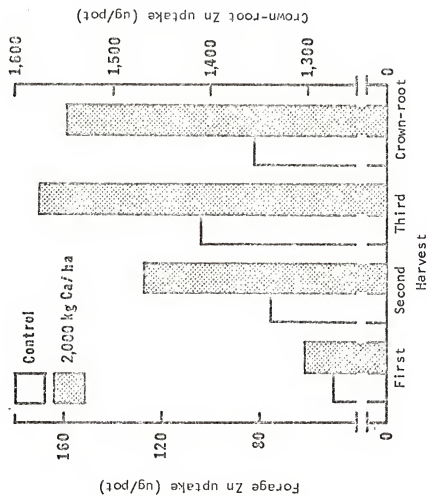
Fig. 13. Relationship between applied Ca and total Zn uptake by jaraguagrass forage and crown-root systems.

Table 11. Effect of applied Zn and N on Zn composition of jaraguagrass forage and crown-root systems.

		Concentration			Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
Treatment [1]	1	2	3		1	2	3
	ppm				ug/pot		
Zn$_0$							
N$_0$	19 a[2]	31 a	35 a	143 abc	36 a	62 a	54 a
N$_1$	20 ab	38 bc	40 ab	106 a	51 bc	104 b	158 b
N$_2$	22 ab	39 bc	40 ab	113 ab	61 cd	118 bc	164 b
Zn$_1$							
N$_0$	19 a	34 ab	36 ab	147 abc	36 a	50 b	42 a
N$_1$	22 ab	40 c	43 bc	146 abc	56 c	108 b	163 b
N$_2$	24 b	45 d	50 de	164 bc	69 d	129 bc	184 bc
Zn$_2$							
N$_0$	23 b	34 ab	39 ab	173 c	42 ab	70 a	62 a
N$_1$	23 b	46 d	47 cd	155 cd	62 cd	146 c	204 c
N$_2$	28 c	49 d	54 e	225 d	80 e	124 bc	202 c

[1] Treatments Zn$_0$, Zn$_1$, and Zn$_2$ were equivalent to 0, 15, and 30 kg Zn/ha; and N$_0$, N$_1$, and N$_2$ to 0, 50, and 100 kg N/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.
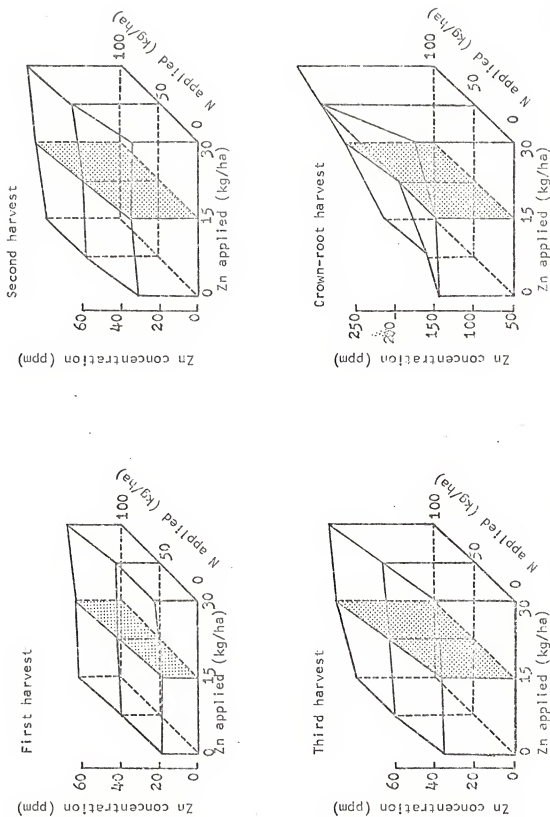
Fig. 14. Relationship between applied Zn and N on Zn concentrations of Jaraguagrass forage and crown-root systems.

and density of developing plants, may have accounted for the low Zn concentrations and lack of response to lower rates of Zn and N.

An overall increase in Zn concentration of the forage was observed by the second harvest and sustained to the third. This was probably due to mineralization of indigenous soil Zn and the general development of larger root systems. Nitrogen, in the absence of applied Zn, significantly increased Zn content of the forage in the second harvest, presumably by its effect on root growth or in lowering soil pH under conditions of rapid hydrolysis and nitrification (213, 237) which could increase availability of indigenous soil Zn. A significant depression in soil pH (KCl) with N applications was found in this study. Although the Zn_1 and Zn_2 treatments increased Zn concentrations of the forage in the second and third harvests, the effect was not significant without the enhancement effect of applied N. Significant, but incipient, N x Zn interactions were found for the last two forage harvests and crown-root harvest. The implication was that the increases in forage or crown-root Zn concentrations from different levels of Zn varied with levels of applied N. The high Zn concentration of 225 ppm for the crown-root systems from the Zn_2N_2 treatment suggested that Zn was accumulating, probably in the form of metallo-protein complexes, since crown-root yields were not different relative to the other Zn and N treatments.

Total Zn uptake by jaraguagrass forage again indicated the synergistic effect of N and Zn although it would appear that the influence of N_1 and N_2 treatments on forage yields was instrumental in increasing Zn uptake in the last two forage harvests (Fig. 15). In absence of N, applied Zn had little influence on Zn uptake by forage in any harvest
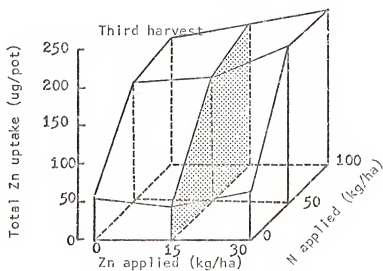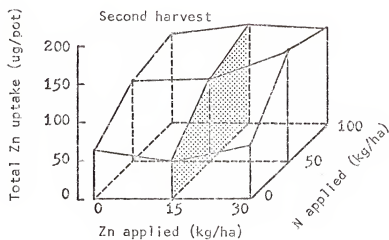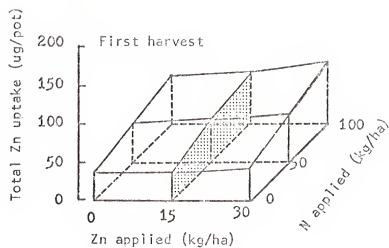
Fig. 15. Relationship between applied Zn and N on total Zn uptake by jaraguagrass forage.

but addition of N_1 treatments resulted in significant and dramatic Zn uptake increases over control, especially for the Zn_2 treatments. Nitrogen (linear) x Zn (linear) and N (quadratic) x Zn (linear) inter-actions were observed in the second harvest, which accounted for dif-ferences in response to Zn treatments over different levels of N.

P x Zn

Data in Table 12 show the effect of P and Zn applications on Zn composition of jaraguagrass. Forage Zn concentrations were only sig-nificantly increased by the Zn_2 treatments irrespective of applied P. A similar response was found for total Zn uptake. Zn concentration of the crown-root systems was significantly increased over control by the Zn_2 treatments although a complementary trend of P could be discerned for the high Zn levels.

Ca x Zn

The effect of Ca and Zn applications on jaraguagrass composition of Zn is shown in Table 13. Calcium, in the form of lime, clearly demonstrated its negative effect on the increase of Zn concentration in forage and crown-root systems even with higher levels of applied Zn (Fig. 16). This antagonistic effect was more pronounced by the last two forage harvests. In the absence of lime, Zn_2 in the first harvest and both Zn_1 and Zn_2 treatments in the last two harvests significantly raised Zn concentration levels in the forage. When lime was applied, Zn concentration of forage in general was lowered by about 7 ppm for Zn-treated plants and only the Zn_2 rate significantly increased Zn values over control. Although lime did depress forage Zn concentration in Zn_0 pots, the 2-3 ppm difference was not statistically significant. Zinc concentration response to Ca and Zn by crown-root systems was similar as for forage.

Table 12. Effect of applied P and Zn on Zn composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				ug/pot		
P$_0$ Zn$_0$	21 a[2]	36 a	39 abc	121 a	48 a	84 a	124 ab
Zn$_1$	23 ab	38 a	44 bcde	146 abc	54 ab	94 a	117 a
Zn$_2$	25 b	45 b	45 cde	182 bcd	57 abc	123 ab	145 abc
P$_1$ Zn$_0$	21 a	38 ab	38 ab	111 a	51 ab	99 ab	121 a
Zn$_1$	21 a	40 ab	44 bcde	151 abc	54 ab	105 ab	140 abc
Zn$_2$	23 ab	44 b	48 e	223 d	62 bc	108 ab	155 bc
P$_2$ Zn$_0$	20 a	35 a	37 a	130 ab	50 a	101 ab	132 ab
Zn$_1$	21 a	41 ab	41 abcd	160 abc	53 ab	88 a	132 ab
Zn$_2$	26 b	40 ab	47 de	188 cd	65 c	109 ab	170 c

[1] Treatments P$_0$, P$_1$, and P$_2$ were equivalent to 0, 50, and 100 kg P/ha; and Zn$_0$, Zn$_1$, and Zn$_2$ to 0, 15, and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 13. Effect of applied Ca and Zn on Zn composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				ug/pot		
Ca0 Zn0	20 a[2]	38 ab	39 ab	131 ab	40 a	66 a	96 a
Zn1	22 ab	43 cd	47 cd	161 b	49 b	74 a	96 a
Zn2	26 c	47 d	50 d	229 c	57 bc	86 bc	121 b
Ca1 Zn0	21 ab	35 a	37 a	110 a	59 c	123 bc	156 c
Zn1	21 ab	36 ab	39 ab	143 ab	58 bc	117 b	163 c
Zn2	24 bc	40 bc	43 bc	167 b	66 c	141 c	191 d

[1]Treatments Ca0 and Ca1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn0, Zn1, and Zn2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

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Fig. 16. Relationship between applied Zn and Ca on Zn concentrations of Jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4, refer to first, second, and third forage harvests and crown-root harvests, respectively).

Total Zn uptake by jaraguagrass forage was enhanced by lime applications especially when the Zn_2 treatment was applied in second and third harvests (Fig. 17). Without lime, Zn applications did significantly increase total Zn uptake by forage in the first harvest but in the subsequent harvest the effect was not significant. Only the Zn_2 rate significantly increased total Zn uptake in the third harvest in lime-free treatments. The dominant influence of lime, both direct and indirect, on increasing forage yields accounts for the apparent effect of lime-induced increase of total Zn uptake. Lime and its effect on Zn availability was complex and can be more readily interpreted in the light of results from soil analysis which will be discussed later.

N x P

Table 14 illustrates the dominant influence of N in increasing both Zn concentration and total uptake of jaraguagrass forage irrespective of P applications. For the first harvest, N_1 and N_2 treatments showed significant differences from each other in raising Zn concentration and total uptake values over control, but in subsequent forage harvests, responses were similar for both levels of N in their significant effect over control. The major effect of N on increasing forage yields and root proliferation probably accounts for the observed data. A number of investigators have observed that crop response to Zn was generally greater when Zn SO_4 was applied with N than with P fertilizers (161, 262). Neither N nor P significantly affected Zn concentration levels of the crown-root systems although a positive trend of increased Zn concentrations with increments of P was noticed in the N_2-treated pots. A general inference would be that N and P while not physiologically altering the ability of the crown-root system to absorb Zn from the soil, may in fact accumulate or immobilize Zn in the system.
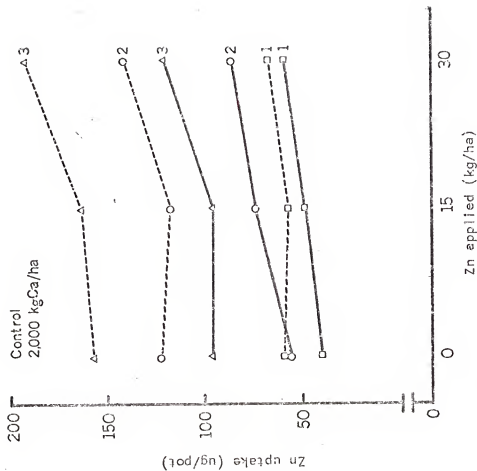
Fig. 17. Relationship between applied Zn and Ca on total Zn uptake by Jaraguagrass forage. (Numbers 1, 2, and 3, refer to first, second, and third forage harvests, respectively).

Table 14. Effect of applied N and P on Zn composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				ug/pot		
N₀							
P₀	21 ab[2]	34 a	35 a	158 a	40 a	65 a	48 a
P₁	20 a	33 a	39 ab	152 a	39 a	61 a	60 a
P₂	19 a	32 a	35 a	152 a	37 a	56 a	50 a
N₁							
P₀	23 ab	41 b	43 bcd	137 a	55 b	115 b	172 b
P₁	20 a	42 bc	43 bc	170 a	54 b	122 b	171 b
P₂	22 ab	41 bc	45 bcd	139 a	60 b	121 b	182 b
N₂							
P₀	25 b	44 bc	50 d	153 a	64 bc	121 b	167 b
P₁	24 b	46 c	48 cd	163 a	74 c	128 b	185 b
P₂	25 b	43 bc	46 cd	185 a	72 c	123 b	198 b

[1] Treatments N₀, N₁, and N₂ were equivalent to 0, 50, and 100 kg N/ha; and P₀, P₁, and P₂ to 0, 50, and 100 kg P/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

N x Ca

Data in Table 15 indicate the effect of applied N and Ca on Zn composition of jaraguagrass. Except for N_2 treatments, Zn concentrations of first harvest forage were not significantly increased by N and Ca treatments. However, subsequent harvests showed the dominant effect of N applications in increasing Zn concentrations of the forage, especially in the absence of lime (Fig. 18). The depressing effect of lime, though ameliorated by N treatments, resulted in forage Zn concentrations of the N_1 treatment level being essentially the same as for control or N_2 treatment responses. Linear N x Ca interactions were observed in the first and third forage harvests which confirm the antagonistic effect of lime in reducing the positive effect of N on increase forage Zn concentrations. The positive and negative effects of N and Ca, respectively, were demonstrated in the Zn concentration responses by crown-root systems although differences were not significant.

A complementary relationship between N and Ca was observed for total Zn uptake by the forage (Fig. 19). Both applied N and Ca significantly increased total forage Zn uptake, especially in the second and third harvests. The synergistic effect of the N_1 or N_2 treatment with lime resulted in 40 to 93% increases in total forage Zn uptake over unlimed pots. Direct and indirect effects of N and Ca, respectively, in increasing growth and yield of jaraguagrass were major factors in total forage Zn uptake.

P x Ca

Lime and its effect on decreasing Zn concentration and increasing total Zn uptake of jaraguagrass forage, irrespective of P levels, is

Table 15. Effect of applied N and Ca on Zn composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				µg/pot		
N_0 Ca_0	20 a[2]	35 a	36 a	158 ab	29 e	48 a	42 a
Ca_1	21 ab	32 a	36 a	151 ab	48 b	73 b	64 a
N_1 Ca_0	22 ab	44 c	47 c	176 b	51 b	92 b	146 b
Ca_1	21 ab	39 ab	40 ab	122 a	62 c	147 c	204 c
N_2 Ca_0	26 c	49 d	53 d	187 b	66 cd	86 b	125 b
Ca_1	23 bc	40 bc	43 bc	148 ab	73 d	161 c	241 d

[1]Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.
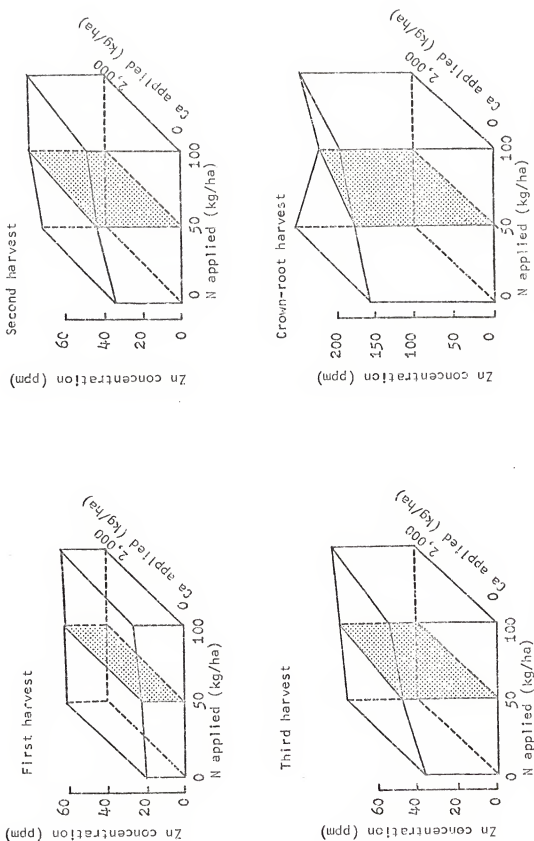
Fig. 18. Relationship between applied N and Ca on Zn concentrations of jaraguagrass forage and crown-root systems.
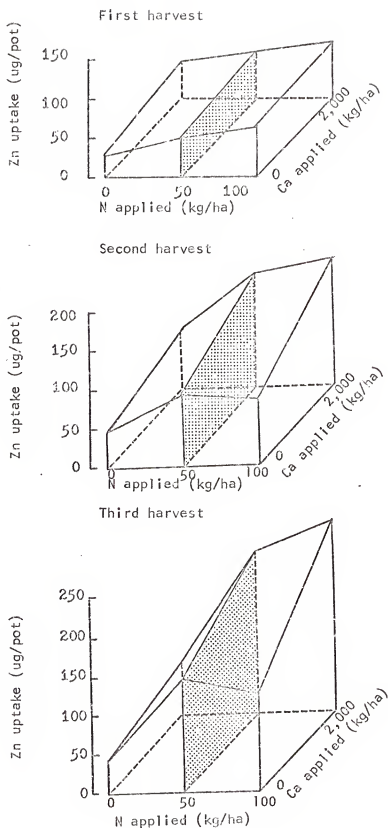
Fig. 19. Relationship between applied N and Ca on total Zn uptake by jaraguagrass forage.

shown in Table 16. Although no significant differences were found in the first forage harvest, lime significantly lowered Zn concentrations of the forage. A similar trend was also shown for Zn concentrations of the crown-root systems although lime significantly showed a depressive effect only at the P_2 level. Total Zn uptake again was significantly increased in the forage at all harvests irrespective of P treatments.

Equations for Zn Composition of Jaraguagrass

Multiple regression equations for Zn composition of jaraguagrass from each harvest are given below for general reference. These equations were calculated using the basic model and coded treatment variables presented in Appendix Table 73 and the coefficients given in Appendix Table 74. The equations are as follows:

Forage Zn (i) = $22 + 2.07x_1 + 2.1x_3 - 0.38x_7 - 1.07x_3x_7$ [1]

Forage Zn (ii) = $40 + 3.44x_1 + 5.54x_3 - 0.88x_4 - 0.29x_7$
$+ 1.85x_3x_1$ [2]

Forage Zn (iii) = $43 + 4.21x_1 + 5.8x_3 - 2.88x_7 + 2.35x_3x_1$
$- 2.44x_3x_7$ [3]

Crown-root Zn (iv) = $157 + 38.44x_1 + 6.46x_3 - 16.84x_7$
$+ 20.39x_3x_1$ [4]

Forage Zn uptake (i) = $55 + 6x_1 + 16x_3 + 6x_7$ [5]

Forage Zn uptake (ii) = $101 + 9x_1 + 32x_3 - 9x_4 + 26x_7$
$+ 0.6x_3x_1 - 6x_4x_1 + 13x_3x_7$ [6]

Table 16. Effect of applied P and Ca on Zn composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				µg/pot		
P_0 Ca_0	24 a[2]	43 b	46 c	170 ab	49 a	72 a	96 a
Ca_1	22 a	37 a	40 ab	131 a	57 ab	129 b	161 b
P_1 Ca_0	22 a	45 b	46 c	188 b	49 a	76 a	102 a
Ca_1	21 a	37 a	40 ab	136 a	62 b	131 b	176 b
P_2 Ca_0	22 a	41 ab	44 bc	164 ab	48 a	78 a	115 a
Ca_1	23 a	37 a	39 a	153 ab	64 b	121 b	172 b

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Forage Zn uptake (iii) = $137 + 15x_1 + 65x_3 - 19x_4 + 33x_7$
$$+ 24x_3x_7 \qquad [7]$$

where Forage Zn (i), (ii), (iii), and Crown-roots (iv) are Zn concentrations in ppm for first, second, and third forage harvests and crown-root system, respectively; Forage Zn uptake (i), (ii), and (iii) are total Zn uptake in ug/pot for three forage harvests, respectively; and x_1, x_3, x_4, and x_7 refer to coded treatment variables Zn (linear), N (linear), N (quadratic), and Ca (linear) in kg/ha, respectively.

In order to determine the level of a nutrient required for maximum Zn concentration or total uptake, linear and quadratic regression coefficients were differentiated, equated to zero, and solved for the specific coded x value. By substitution, the x value was converted to the nutrient level in kg/ha (Appendix Table 73). For example, the calculated level of N required for maximum Zn uptake by jaraguagrass forage was 130 kg N/ha for both the second and third harvests. Maximum Zn uptake by forage with N applications was therefore not realized for the duration of this study.

In general, forage Zn concentrations of jaraguagrass were significantly increased by Zn and N applications in all three harvests. The effect was more pronounced for the second and third forage harvests and with higher levels of Zn (30 kg Zn/ha equivalent) and N (100 kg N/ha/harvest equivalent). Overall increase in Zn concentrations of forage from first to second harvest was attributed to various factors that increased the availability of soil Zn and to the physiological development of the plant and its rooting system. Positive, but incipient, N x Zn interactions were observed for the last two forage harvests. Nitrogen, as urea, increased forage Zn concentrations by its

effect on stimulating root proliferation and by lowering soil pH under conditions of rapid hydrolysis and nitrification.

Phosphorus showed little effect on forage Zn concentrations. With the exception of the first harvest, Ca significantly depressed forage Zn concentrations partly by its adverse effect on Zn availability in the soil and partly by dilution effect of the lime-induced yield increases. Negative N x Ca interactions on forage Zn concentration were found for the first and third harvests. These were primarily attributed to the dilution effect of higher yields.

Zinc concentrations of the crown-root systems were significantly increased by Zn applications and by an incipient but positive effect of N and a N x Zn interaction. Lime also depressed Zn concentrations in the crown-root systems.

Total forage Zn uptake was significantly increased by Zn, N, and Ca. The main effect of N and Ca was in increasing forage yields. A negative N (quadratic) effect for the second and third forage harvests and a N x Zn interaction in the second harvest suggested that the N_2 treatment had a toxic effect on the roots or that Zn was being accumulated in the crown-root system. Phosphorus again showed no effect on total forage Zn uptake.

Although absolute values reported for total Zn uptake in the crown-root systems were not corrected for possible soil contamination, they did indicate quite dramatically the positive effect of Zn, N, P, and Ca on increasing total Zn uptake. At high rates of N and P, Zn may have been accumulated or immobilized in the crown-root systems.

Phosphorus Concentration and Total Uptake

Phosphorus concentrations of jaraguagrass ranged from 400 to 2,000,

525 to 3,500, 475 to 3,075, and 87 to 2,000 ppm for the first, second, and third forage harvests and crown-root systems, respectively. Average forage P concentrations were 986, 1,473, and 1,285 ppm for the three harvests, respectively, while crown-root systems averaged 533 ppm P. These values are similar or slightly lower than those reported elsewhere and for the Santa Fe field studies reported herein. Blue et al. (23) reported an average value of 2,800 ppm P for jaraguagrass forage sampled at Santa Fe and 1,300 ppm P at Patino, eastern Panama. Ranges of 500 to 1,900 ppm P for jaraguagrass forage and 600 to 1,200 ppm P for roots were given for dry season samples from Costa Rica but rainy season forage values ranged from a low 800 to 1,000 ppm (243).

Average total P uptake values for jaraguagrass were 2.37, 3.61, 3.62, and 4.89 mg/pot (equivalent to 1.29, 1.96, 1.97 and 2.66 kg P/ha) for the three forage harvests and crown-root systems, respectively. Reports of 2.40 to 15.70 mg P/pot equivalent for total P uptake by jaraguagrass forage and 2.20 to 7.72 mg P/pot for roots (243) suggest that the average values obtained in this study were comparatively low.

Main treatment effects

Main treatment effects on P composition of jaraguagrass are summarized in Table 17.

Response to Zn.--Except for the third forage harvest, Zn fertilizer levels did not significantly affect P concentration nor total P uptake of jaraguagrass forage and crown-root systems. In the third harvest, Zn_2 treatment level significantly increased forage P concentration over Zn_1 and control but the control values were significantly higher than those from the Zn_1 treatment rate. The Zn_1 treatment also lowered P concentrations of the crown-root systems, though not significantly.

Table 17. Main effects of applied Zn, N, P, and Ca on P composition of jaraguagrass forage and crown-root systems.

	Concentration				Total uptake			
	Forage harvest			Crowns and roots	Forage harvest			Crowns and roots
Treatment[1]	1	2	3		1	2	3	
	ppm				mg/pot			
Zn_0	960 a[2]	1,450 a	1,280 b	580 a	2.26 a	3.62 a	3.64 ab	5.08 a
Zn_1	1,040 a	1,470 a	1,220 a	490 a	2.49 a	3.33 a	3.24 a	4.54 a
Zn_2	960 a	1,500 a	1,350 c	540 a	2.34 a	3.87 a	3.99 a	5.08 a
N_0	1,160 b	2,060 b	1,860 c	550 a	2.18 a	3.82 a	2.64 a	3.76 a
N_1	870 b	1,190 a	1,040 b	510 a	2.32 a	3.54 a	4.34 b	5.44 b
N_2	920 a	1,170 a	950 a	540 a	2.61 b	3.46 a	3.88 b	5.48 b
P_0	920 a	1,240 b	1,090 a	450 a	2.08 a	3.04 a	2.78 a	3.88 a
P_0	1,000 ab	1,470 b	1,330 b	520 ab	2.50 b	3.67 b	3.93 b	5.21 b
P_2	1,040 b	1,720 c	1,430 c	630 b	2.52 b	4.11 b	4.16 b	5.59 b
Ca_0	920 a	1,310 a	1,210 a	510 a	1.87 a	2.20 a	2.39 a	3.82 a
Ca_1	1,050 b	1,630 b	1,360 b	560 a	2.87 b	5.02 b	4.85 b	5.97 b

[1] Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha; P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

Similarly, mean total forage P uptake with the Zn_1 rate was signifi-
cantly lower than Zn_2 at the third harvest. This was a reflection
of the lower oven-dry yield for the corresponding treatments.

Response to N.--Nitrogen significantly (P = 0.01) decreased forage
P concentrations from control by over 20, 40, and 45% for the three
forage harvests, respectively. By the third harvest, the N_2 rate
significantly lowered forage P concentration from the N_1 rate. The P
concentration depression was mainly due to the dilution effect of
forage yield increases by N. Total P uptake by forage was significantly
increased by the N_2 rate in the first harvest and by both N_1 and N_2
rates in the third harvest. No significant effect of N on total forage
P uptake was found in the second harvest when the concentration depres-
sion and forage yield increase by N were nullified. Phosphorus con-
centration of the crown-root systems were not affected by N increments,
but the N_1 and N_2 rate significantly increased total P uptake. The
positive effect of N on increasing P uptake by plants may have been a
result of stimulating root development or changing the characteristic
of plant roots so that P was more rapidly absorbed (75).

Response to P.--Both P concentration and total uptake values were
significantly (P = 0.01) increased with P applications (Figs. 20 and
21). Nonsignificant P concentration differences between P_1 treatment
and control or P_2 could be attributed to the difficulty in obtaining
a homogeneous mixture of P fertilizer and soil, general immobility of
P in the soil through various fixation processes, and underdeveloped
plant roots. A general increase in P concentration of forage was
observed by the second harvest suggesting that some indigenous soil P
may have been made available to plants through mineralization of in-

Fig. 20. Relationship between applied P and P concentrations of jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4 refer to first, second, and third forage harvests and crown-root harvests, respectively).

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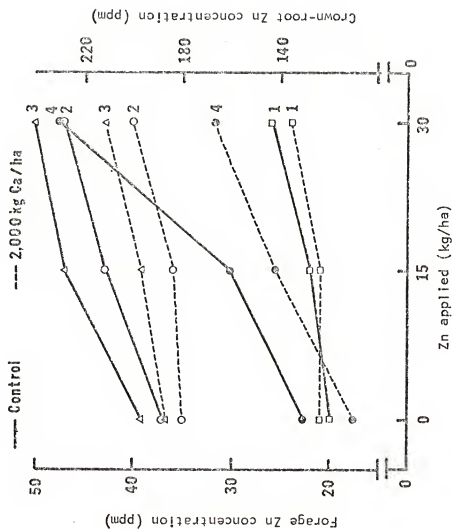

Fig. 21. Relationship between applied P and total P uptake by jaraguagrass forage and crown-root systems. (Numbers 1, 2, 3, and 4 refer to first, second, and third forage harvests and crown-root harvests, respectively).

organic P, organic matter decomposition and associated reactions or increased rooting volume and density.

Total forage P uptake was significantly increased over control in all three harvests by both the P_1 and P_2 rates which, because of similarity of forage yields, were not significantly different from each other. Higher total P uptake values in the second harvest over the first were a result of the general increase in P absorption by jeraguagrass.

Phosphorus applied at the highest rate significantly increased P concentration of the crown-root systems over control while both P_1 and P_2 rates significantly increased total P uptake. This increase in total P uptake with P application was due mainly to the higher P concentrations in the crown-root systems.

Response to Ca.--Calcium consistently resulted in higher forage P concentrations and total uptake (Figs. 22 and 23), mainly through its effect on various soil factors, such as raising pH to a level that resulted in maximum availability of phosphate and other nutrients. Actual levels of forage P concentration in the forage, though significant, were not appreciably higher than control by liming but total P uptake was dramatically increased over control by 53, 128, and 107% for the three forage harvests, respectively. This was a reflection of the increased forage yields.

Although crown-root P concentrations were not significantly increased by liming, total P uptake was increased by 30% over control. Again higher yields for lime-treated plants were primarily responsible for the significance recorded.

Fig. 22. Relationship between applied Ca and P concentrations of jaraguagrass forage and crown-root systems.
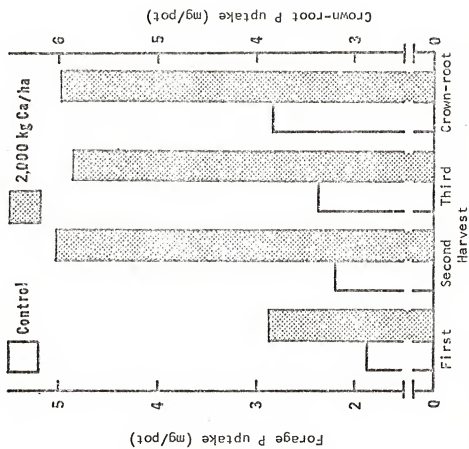
Fig. 23. Relationship between applied Ca and total P uptake by jaraguagrass forage and crown-root systems.

Zn x N

The effect of Zn and N applications on P composition of jaragua-grass is presented in Table 18. Nitrogen significantly decreased P concentration in the forage irrespective of Zn levels. Neither Zn or N affected P concentration in the crown-root systems. Total P uptake was not appreciably increased by N until the third forage harvest.

Numerous interactions (Appendix Table 74) influenced total P uptake by forage in the third harvest making interpretations of response in two-way tables difficult. For example, an incipient positive effect of Zn was observed but its effect was nullified by negative N x Zn interactions.

P x Zn

In the absence of applied P, Zn showed a trend of raising P concentrations of the forage which was not significant until the third harvest (Table 19). Phosphorus had an overriding influence in increasing forage P concentration in the second and third harvests. No consistent effect of P or Zn could be discerned from the total forage P uptake data due to the many interaction effects with other nutrients. Crown-root P concentrations did not respond to P and Zn in a meaningful way.

Ca x Zn

The effect of Ca in increasing forage P composition was dominant and significant over Zn treatments (Table 20). In contrast, the crown-root systems showed no response to Ca and Zn treatments.

N x P

Phosphorus increased P concentration of both forage and crown-root systems significantly in the absence of N (Table 21). A general

Table 18. Effect of applied Zn and N on P composition of Jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pot		
Zn$_0$[2] N$_0$	1,140 b	2,010 b	1,940 d	580 a	2.18 a	4.04 a	3.08 bc
N$_1$	850 a	1,150 a	980 a	540 a	2.15 a	3.18 a	3.96 c
N$_2$	890 a	1,200 a	930 a	620 a	2.45 ab	3.64 a	3.87 c
Zn$_1$ N$_0$	1,210 b	2,080 b	1,700 c	460 a	2.24 a	3.19 a	1.89 a
N$_1$	940 a	1,220 a	1,010 a	550 a	2.44 ab	3.39 a	3.99 c
N$_2$	980 a	1,100 a	950 a	450 b	2.81 b	3.41 a	3.84 c
Zn$_2$ N$_0$	1,160 b	2,090 b	1,950 d	610 a	2.11 a	4.21 a	2.95 b
N$_1$	830 a	1,200 a	1,140 b	440 a	2.36 ab	4.06 a	5.08 c
N$_2$	890 a	1,200 a	970 a	550 a	2.56 ab	3.35 a	3.93 c

[1] Treatments Zn$_0$, Zn$_1$, and Zn$_2$ were equivalent to 0, 15, and 30 kg Zn/ha; and N$_0$, N$_1$, and N$_2$ to 0, 50, and 100 kg N/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 19. Effect of applied P and Zn on P composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pot		
P_0							
Zn_0	900 a[2]	1,100 a	1,060 a	500 ab	2.03 a	2.58 a	2.78 a
Zn_1	940 a	1,280 ab	1,070 ab	470 ab	2.16 ab	2.88 ab	2.61 a
Zn_2	920 a	1,330 a	1,150 bc	380 a	2.06 a	3.67 ab	2.96 ab
P_1							
Zn_0	960 ab	1,570 bc	1,370 d	570 ab	2.34 abc	3.97 c	3.98 bc
Zn_1	1,060 ab	1,370 ab	1,160 c	350 a	2.65 bc	3.46 abc	3.28 abc
Zn_2	970 ab	1,460 bc	1,470 c	650 b	2.52 abc	3.58 abc	4.52 c
P_2							
Zn_0	1,020 ab	1,690 c	1,410 de	670 b	2.42 abc	4.31 c	4.15 bc
Zn_1	1,130 b	1,750 c	1,430 de	630 b	2.67 c	3.66 bc	3.84 abc
Zn_2	990 ab	1,710 c	1,450 de	580 ab	2.46 abc	4.37 c	4.48 c

[1]Treatments P_0, P_1 and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Zn_0, Zn_1 and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 20. Effect of applied Ca and Zn on P composition of jaraguagrass forage and crown-root systems.

		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
Treatment[1]		1	2	3		1	2	3
		ppm				mg/pot		
Ca_0	Zn_0	900 ab[2]	1,330 a	1,160 a	520 a	1.74 a	2.36 a	2.42 ab
	Zn_1	1,000 abc	1,250 a	1,170 a	480 a	2.04 c	1.97 a	1.99 a
	Zn_2	870 a	1,360 ab	1,310 b	540 a	1.81 a	2.26 a	2.78 b
Ca_1	Zn_0	1,010 bc	1,580 bc	1,400 c	640 a	2.78 b	4.88 b	4.85 c
	Zn_1	1,080 c	1,690 c	1,270 b	490 a	2.95 b	4.69 b	4.50 c
	Zn_2	1,050 c	1,630 c	1,400 c	540 a	2.88 b	5.49 b	5.20 c

[1] Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 21. Effect of applied N and P on P composition of jaraguagrass forage and crown-root systems.

| | | Concentration | | | Total uptake | | |
| | Forage harvest | | | Crowns and roots | Forage harvest | | |
Treatment[1]	1	2	3		1	2	3
	--- ppm ---				--- mg/pot ---		
N_0							
P_0	1,020 a[2]	1,710 c	1,730 d	450 a	1.83 a	3.25 ab	2.39 a
P_1	1,190 b	2,070 d	1,670 d	520 a	2.28 abc	4.06 b	2.34 a
P_2	1,300 b	2,400 c	2,190 c	680 b	2.43 bc	4.14 b	3.19 ab
N_1							
P_0	850 a	1,040 a	803 a	410 a	2.09 ab	3.09 ab	3.31 b
P_1	860 a	1,150 ab	1,250 c	530 a	2.32 bc	3.51 ab	5.05 c
P_2	920 a	1,380 b	1,080 b	590 a	2.53 bcd	4.03 b	4.67 c
N_2							
P_0	890 a	950 a	740 a	430 a	2.32 bc	2.79 a	2.64 ab
P_1	940 a	1,170 ab	1,080 b	520 a	2.91 d	3.44 ab	4.39 c
P_2	920 a	1,370 b	1,030 b	610 a	2.60 cd	4.17 b	4.61 c

[1] Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha; and P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

depression in P concentration of plant tissues was caused by the dilution effect of yield increases by N applications. Only in the second and third harvests did P show significant effects in elevating P concentration levels of the forage although the values were significantly lower than P treatments without N. Nitrogen x P interactions were observed for the first and third harvests.

A complementary effect of N and P in increasing total forage P uptake values was revealed. The significant increase in total P uptake by P was only noticeable in presence of N at the third harvest.

N x Ca

Nitrogen applications had a dominant influence in depressing forage P concentrations significantly even with additions of lime. Lime increased forage P concentrations significantly by the second and third harvests but its influence with each increment of N was dramatically suppressed (Table 22). Lime, however, had an overriding effect over N in the increasing total forage P uptake. The complementary effect of N was not overt until the third harvest. A positive N x Ca interaction was also recorded for the third harvest. Neither N nor lime significantly changed P concentrations of the crown-root systems.

P x Ca

Table 23 shows the synergistic effect of P and lime in increasing both P concentration and total uptake values in forage, especially in the second and third harvests when P x Ca interactions were positively significant. The P_2Ca_1 treatments gave highest forage P composition values. Lime was the dominant factor in total P uptake. Total P uptake was generally higher than control by 100% with lime applications

Table 22. Effect of applied N and Ca on P composition of jaraguagrass forage and crown-root systems.

Treatment[1]		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
		1	2	3		1	2	3
		ppm				mg/pot		
N0	Ca0	1,170 c[2]	1,900 d	1,800 d	510 a	1.73 a	2.64 a	2.08 a
	Ca1	1,170 c	2,230 e	1,930 e	590 a	2.63 c	4.99 b	3.20 c
N1	Ca0	740 a	980 a	934 ab	540 a	1.70 a	2.03 a	2.86 bc
	Ca1	1,000 b	1,400 c	1,150 c	480 a	2.93 cd	5.05 b	5.83 d
N2	Ca0	860 a	1,060 ab	910 a	490 a	2.17 b	1.92 a	2.25 ab
	Ca1	730 a	1,270 bc	990 b	590 a	3.05 d	5.01 b	5.52 d

[1]Treatments N0, N1, and N2 were equivalent to 0, 50, and 100 kg N/ha; and Ca0 and Ca1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 23. Effect of applied P and Ca on P composition of jaraguagrass forage and crown-root systems.

		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
Treatment[1]		1	2	3		1	2	3
		ppm				mg/pot		
P_0	Ca_0	880 a[2]	1,170 a	1,030 a	500 abc	1.71 a	1.91 a	1.75 a
	Ca_1	950 ab	1,310 ab	1,150 b	400 a	2.45 b	4.17 b	3.80 c
P_1	Ca_0	910 a	1,320 ab	1,370 d	450 ab	1.92 a	2.14 a	2.84 b
	Ca_1	1,080 bc	1,610 c	1,300 c	600 bc	3.09 c	5.20 c	5.02 d
P_2	Ca_0	970 ab	1,460 bc	1,240 c	590 bc	1.97 a	2.54 a	2.59 b
	Ca_1	1,120 c	1,980 d	1,620 e	660 c	3.07 c	5.69 c	5.72 e

[1] Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

while the addition of P_1 or P_2 resulted in further increases of about 40%. Phosphorus only significantly increased total P uptake over control in the third harvest when lime was not added.

Multiple regression equations for the relationship between applied nutrients and P composition of jaraguagrass forage and crown-root systems could be expressed using the model and appropriate coefficients presented in Appendix Tables 73 and 74, respectively.

Forage P concentration was generally increased by P fertilizer although its effect was not fully significant until the last two harvests. Lime also increased forage P concentrations mainly by its influence on plant growth through numerous soil fertility factors including raising soil pH, increasing availability of most plant nutrients, reducing toxicity of Al, Fe, and Mn, and stimulating microbial activity. These benefical effects outweighed the depressive influence of lime on available soil P.

The appreciable depression of forage P concentrations by N from harvest to harvest was mainly due to a dilution effect resulting from increased yields. Interactions between N and P were significant for the first and second harvests. Zinc showed little effect on P concentrations of forage although a positive trend was observed for the Zn_2 rate by the third harvest.

Phosphorus applications significantly stimulated total forage P uptake in all three harvests but no differences were found between P_1 and P_2 treatments. Indirect and direct effects of lime and the N_2 treatment level of raising forage yields were contributory in increasing total P uptake. Zinc again did not exhibit any appreciable influence on P uptake until the third harvest when a positive effect was exerted.

With the exception of P, applied nutrients had little effect on P concentrations of the crown and root systems. However, P, N, and lime did increase total P uptake by the crown-root systems over control. The influence of lime and N was again a reflection of their effect on yields.

Calcium Concentration and Total Uptake

Calcium concentration values ranged from 2,750 to 7,880, 2,250 to 8,800, 3,500 to 11,000, and 986 to 4,900 ppm for the three jaraguagrass forage harvests and crown-root systems, respectively. Average Ca concentration of the three forage and crown-root harvests was 4,950, 5,390, 5,410, and 3,300 ppm, respectively. There was little difference in forage Ca concentrations after the first harvest which gave 9% lower values than subsequent harvests. Total Ca uptake averaged 11.80, 13.62, 16.30, and 31.90 mg/pot (equivalent to 6.42, 7.41, 8.87, and 17.35 kg Ca/ha) for the three forage harvests and crown-root systems, respectively. These forage Ca concentration values are higher than those reported by Blue et al. (23) for jaraguagrass in Panama. Tergas (243) gave a range of 5,100 to 7,500 ppm Ca in jaraguagrass forage harvested during the rainy season in Costa Rica.

Main treatment effects

Table 24 summarizes the main effects of applied nutrients on Ca composition of jaraguagrass.

Response to Zn.--Applied Zn did not significantly affect Ca composition of the jaraguagrass crown-root systems or the first and second forage harvests. In the third harvest, application of Zn significantly increased Ca concentration of forage. This was due partly, to an abnormally high Ca concentration value of 11,000 ppm for the Zn_1 treat-

Table 24. Main effects of applied Zn, N, P, and Ca on Ca composition of jaraguagrass forage and crown-root systems.

Treatment [1]	Concentration				Total uptake			
	Forage harvest			Crowns and roots	Forage harvest			Crowns and roots
	1	2	3		1	2	3	
	ppm				mg/pot			
Zn_0	4,990 a [2]	5,410 a	5,170 a	3,210 a	11.70 a	14.01 a	16.17 a	30.14 a
Zn_1	4,930 a	5,370 a	5,520 b	3,390 a	11.75 a	12.67 a	15.25 a	32.12 a
Zn_2	4,940 a	5,390 a	5,540 b	3,310 a	11.95 a	14.18 a	17.47 b	33.43 a
N_0	5,810 b	6,440 b	6,410 b	3,210 a	10.82 a	12.37 a	9.26 a	22.59 a
N_1	4,550 a	4,960 a	4,810 a	3,280 a	11.99 b	14.59 b	19.65 b	37.60 c
N_2	4,460 a	4,760 a	5,010 a	3,410 a	12.59 b	13.89 a	19.98 b	35.41 b
P_0	5,050 a	5,320 a	5,320 a	3,310 a	11.30 a	13.26 a	15.05 a	31.72 a
P_1	4,920 a	5,440 a	5,490 a	3,350 a	12.19 b	14.15 a	16.81 b	32.74 a
P_2	4,880 a	5,400 a	5,420 a	3,250 a	11.90 ab	13.45 a	17.04 b	31.23 a
Ca_0	4,680 a	4,990 a	5,080 a	3,060 a	9.40 a	8.75 a	10.60 a	23.21 a
Ca_1	5,230 b	5,780 b	5,740 b	3,540 b	14.19 b	18.49 b	22.00 b	40.58 b

[1] Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha; P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

ment pots and partly to an incipient Zn x P interaction. The Zn_2 rate significantly increased total forage Ca uptake of the third harvest mainly because of an incipient Zn x N interaction.

Response to N.--Nitrogen significantly (P = 0.01) depressed Ca concentration in the forage over control due essentially to the dilution effect of increased yields (Fig. 24). Nitrogen x Ca interactions were significant (P = 0.01) for the three forage harvests. Total Ca uptake was significantly increased by N, although only the N_1 rate differed from control significantly in the second forage harvest (Fig. 25). A significant (P = 0.01) N x Ca interaction was observed for total forage Ca uptake at the third harvest.

Crown-root Ca concentrations were not significantly raised by N but total Ca uptake values were increased significantly by N_1 and N_2 rates over control. Again the increases were attributed to corresponding higher yields.

Response to P.--No significant response was shown for Ca concentration of forage or crown-root systems by P applications but the P_1 rate and both P_1 and P_2 rates significantly increased total Ca uptake in forage for the first and third harvests, respectively. Since yield and Ca concentration values were similar, total Ca uptake by the crown-root systems were also insignificant.

Response to Ca.--As expected, lime significantly (P = 0.01) increased Ca concentration and total uptake in the forage and crown-root systems (Figs. 26 and 27). While lime increased Ca concentrations of forage and crown-root systems over control by between 12-16%, total Ca uptake values were dramatically increased by between 50-110% as a result of concomitant yield increases.
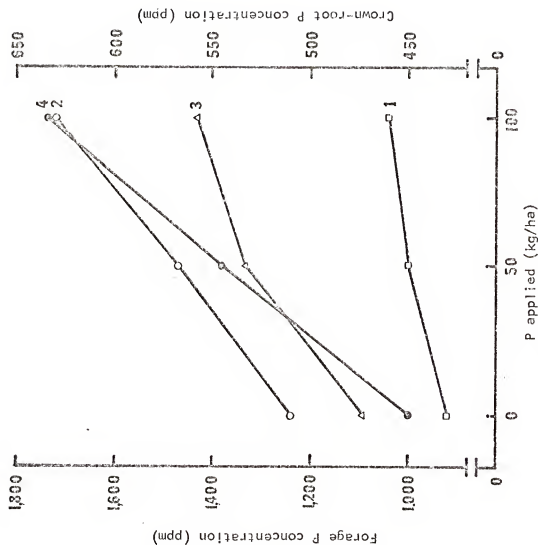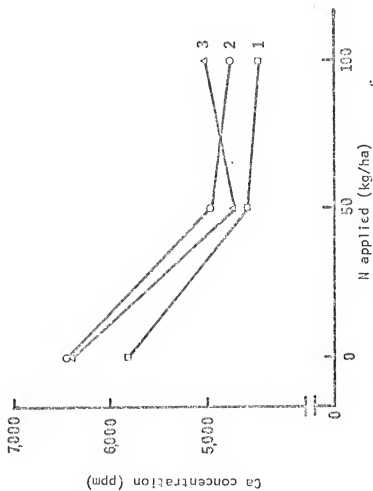
Fig. 24. Relationship between applied N and Ca concentration of jaraguagrass forage. (Numbers 1, 2, and 3 refer to first, second and third forage harvests, respectively).
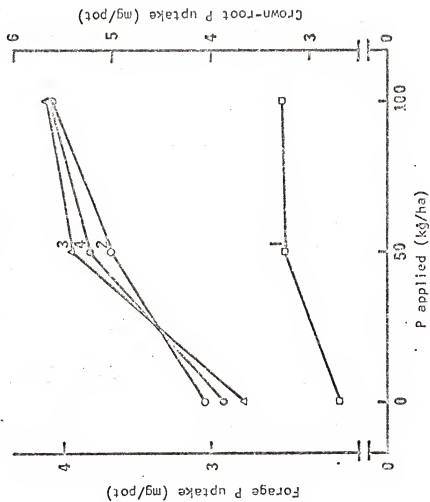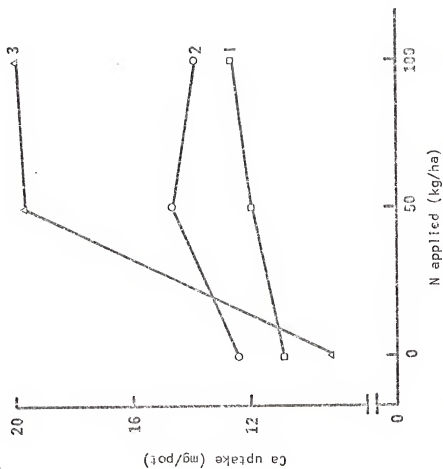
Fig. 25. Relationship between applied N and total Ca uptake by Jaraguagrass forage. (Numbers 1, 2, and 3 refer to first, second, and third harvests, respectively).
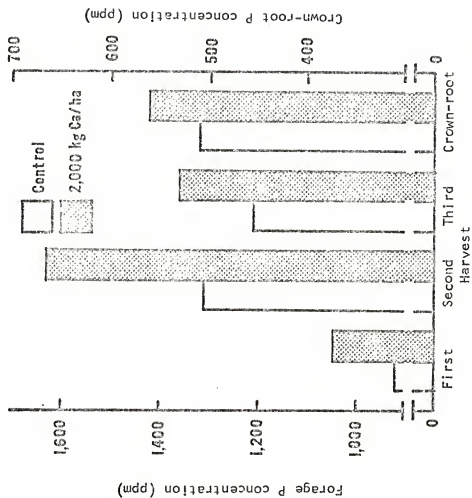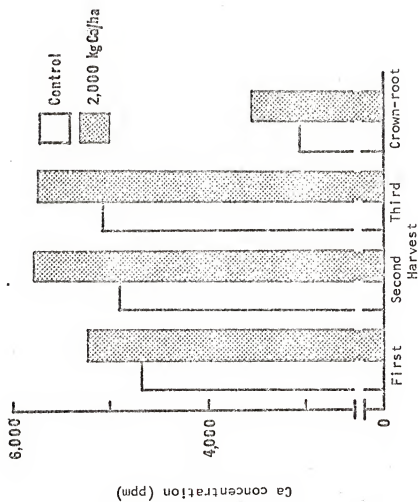
Fig. 26. Relationship between applied Ca and Ca concentrations of jaraguagrass forage and crown-root systems.
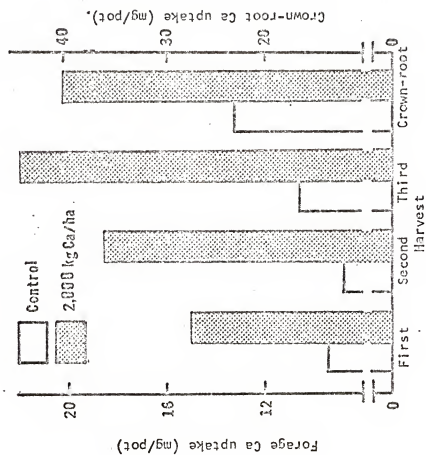
Fig. 27. Relationship between applied Ca and total Ca uptake by jaraguagrass forage and crown-root systems.

Zn x N

Table 25 shows that the effect of applied Zn and N was dominated by N in decreasing forage Ca concentrations and in increasing total Ca uptake. Zinc significantly increased Ca uptake in the second forage harvest in the presence of the N_1 treatment. Incipient Zn x N interactions, involving both negative Zn (linear) and positive Zn (quadratic) effect with N (linear), were observed.

A significant (P = 0.01) effect of Zn was recorded in the third forage harvest in increasing Ca uptake but was essentially a reflection of the differences in forage yields. Crown-root systems showed little response to Zn or N.

P x Zn

Forage Ca composition was not consistently responsive to P and Zn applications although the Zn_1 and Zn_2 treatments did show slightly higher total Ca uptake values in the presence of P at the third harvest (Table 26). Crown-root systems again showed no predictable Ca concentrations attributable to P and Zn applications.

Ca x Zn

Table 27 illustrates the dominant influence of lime over Zn treatments in elevating Ca concentration values of jaraguagrass forage and crown-root systems. Zinc again significantly increased Ca concentrations in the third forage harvest. Lime in its effect on forage yields doubled the total Ca uptake in the second and third forage harvests and Zn was observed to have a complementary effect.

N x P

It was evident from Table 28 that N decreased forage Ca concentration irrespective of P levels. Similarly, N was dominant by stimulating forage yields in significantly increasing total Ca uptake values.

Table 25. Effect of applied Zn and N on Ca composition of jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pot		
Zn0 N0	5,790 b[2]	6,360 b	6,230 c	2,910 a	11.00 a	13.27 b	9.77 a
N1	4,670 a	5,070 a	4,670 ab	3,290 ab	11.66 ab	13.94 b	19.21 bc
N2	4,520 a	4,780 a	4,600 a	3,420 ab	12.43 b	14.81 b	19.54 bc
Zn1 N0	5,730 b	6,590 b	6,530 c	3,480 b	10.65 a	10.10 a	7.76 a
N1	4,660 a	4,900 a	4,720 ab	3,240 ab	11.97 ab	13.92 b	18.11 b
N2	4,390 a	4,610 a	5,310 b	3,440 ab	12.63 b	13.98 b	19.89 bc
Zn2 N0	5,890 b	6,370 b	6,470 c	3,240 ab	10.80 a	13.73 b	10.26 a
N1	4,450 a	4,920 a	5,020 ab	3,320 ab	12.35 b	15.92 b	21.63 c
N2	4,470 a	4,890 a	5,120 ab	3,350 ab	12.70 b	12.89 b	20.52 bc

[1] Treatments Zn_0, Zn_1 and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; and N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 26. Effect of applied P and Zn on Ca composition of Jaraguagrass forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pot		
P_0 Zn_0	5,130 bc[2]	5,340 a	5,330 ab	3,160 a	11.39 a	12.99 ab	15.83 ab
Zn_1	4,910 abc	5,330 a	5,410 ab	3,400 a	11.17 a	12.53 ab	13.58 a
Zn_2	5,130 bc	5,300 a	5,210 a	3,350 a	11.34 a	14.27 ab	15.73 ab
P_1 Zn_0	5,260 c	5,430 a	4,960 a	3,360 a	12.53 a	13.97 ab	15.65 ab
Zn_1	4,790 abc	5,390 a	5,560 ab	3,450 a	11.96 a	14.13 ab	15.88 ab
Zn_2	4,700 ab	5,500 a	5,950 b	3,230 a	12.08 a	14.34 ab	18.89 c
P_2 Zn_0	4,580 a	5,440 a	5,210 a	3,110 a	11.17 a	15.05 b	17.03 bc
Zn_1	5,080 abc	5,380 a	5,580 ab	3,300 a	12.11 a	11.34 a	16.30 abc
Zn_2	4,990 abc	5,370 a	5,460 ab	3,330 a	12.43 a	13.95 ab	17.78 bc

[1] Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 27. Effect of applied Ca and Zn on Ca composition of jaraguagrass forage and crown-root systems.

		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
Treatment[1]		1	2	3		1	2	3
		-------- ppm --------				-------- mg/pot --------		
Ca_0	Zn_0	4,730[2]	5,040 a	4,710 a	3,080 a	9.07 a	9.02 a	10.66 a
	Zn_1	4,690 a	4,920 a	5,270 b	3,160 a	9.60 a	8.31 a	9.59 a
	Zn_2	4,610 a	5,020 a	5,250 b	2,940 a	9.54 a	8.91 a	11.55 a
Ca_1	Zn_0	5,250 b	5,770 b	5,620 bc	3,340 ab	14.32 b	18.99 bc	21.69 bc
	Zn_1	5,170 b	5,810 b	5,770 c	3,610 b	13.89 b	17.03 b	20.92 b
	Zn_2	5,260 b	5,760 b	5,830 c	3,680 b	14.37 b	19.45 c	23.39 c

[1] Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1 and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 28. Effect of applied N and P on Ca composition of jaraguagrass forage and crown-root systems.

Treatment[1]		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
		1	2	3		1	2	3
		ppm				mg/pot		
N_0	P_0	5,900 b[2]	6,310 b	6,260 b	3,320 a	10.68 a	12.47 ab	8.74 a
	P_1	5,790 b	6,640 b	6,460 b	3,270 a	11.07 ab	13.29 ab	9.64 a
	P_2	5,720 b	6,510 b	5,510 b	3,050 a	10.70 a	11.34 a	9.41 a
N_1	P_0	4,700 a	4,910 a	4,650 a	3,290 a	11.54 abc	14.12 ab	19.10 bc
	P_1	4,580 a	4,960 a	4,350 a	3,370 a	12.19 bcd	14.87 b	19.53 bc
	P_2	4,490 a	5,010 a	4,920 a	3,190 a	12.25 bcd	14.79 b	20.32 c
N_2	P_0	4,560 a	4,750 a	5,040 a	3,320 a	11.69 abc	13.19 ab	17.31 b
	P_1	4,380 a	4,720 a	5,170 a	3,390 a	13.32 d	14.29 ab	21.25 c
	P_2	4,440 a	4,810 a	4,820 a	3,510 a	12.76 cd	14.20 ab	21.40 c

[1] Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha; and P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Phosphorus, however, demonstrated an incipient negative effect in the first forage harvest in lower Ca concentrations, mainly through its contribution in forage yield increases of that harvest. Neither N or P influenced Ca concentrations of crown-root systems.

N x Ca

Nitrogen x Ca interactions were deemed significant ($P = 0.01$ for first and second harvests and $P = 0.05$ in the third harvest) for forage Ca concentrations in all harvests and for total Ca uptake ($P = 0.01$) in the third harvest (Table 29). Nitrogen appeared to have a significant and profound effect in depressing Ca forage concentrations although lime ameliorated this effect significantly compared to unlimed treatments, especially in absence of N for the last two forage harvests. A complementary effect of N and Ca was observed in increasing total forage Ca uptake. Lime, however, had an overriding and significant effect over N in increasing total Ca uptake by two-fold over unlimed treatments.

Calcium concentrations of the crown-root systems were not affected by N applications in the absence of lime but did overtly depress the positive effect of lime on Ca concentration increases.

P x Ca

Data in Table 30 indicate that lime increased both Ca concentrations and total uptake in forages and crown-root systems over control and P treatments. Significant ($P = 0.05$) and positive P x Ca interactions were observed for the first and third forage harvests. In presence of lime, P treatments enhanced Ca concentration values in the forage presumably by their stimulative effect on root development, particularly of lateral and fibrous rootlets.

Table 29. Effect of applied N and Ca on Ca composition of jaraguagrass forage and crown-root systems.

Treatment[1]		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
		1	2	3		1	2	3
		ppm				mg/pot		
N_0	Ca_0	5,810 c[2]	5,810 b	5,330 c	3,080 ab	8.61 a	8.10 a	6.69 a
	Ca_1	5,810 c	7,080 c	7,000 d	3,340 ab	13.02 c	16.63 b	11.83 b
N_1	Ca_0	4,060 a	4,550 a	4,470 a	3,030 a	9.14 a	9.62 a	13.59 b
	Ca_1	5,120 b	5,300 b	5,140 b	3,540 bc	14.84 d	19.57 d	25.71 c
N_2	Ca_0	4,170 a	4,630 a	4,940 ab	3,070 a	10.46 b	8.52 a	11.52 b
	Ca_1	4,750 b	4,900 a	5,080 b	3,750 c	14.71 d	19.27 d	28.50 d

[1]Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 30. Effect of applied P and Ca on Ca composition of jaraguagrass forage and crown-root systems.

Treatment[1]		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
		1	2	3		1	2	3
		ppm				mg/pot		
P_0	Ca_0	4,960 b[2]	5,010 a	5,140 ab	2,930 a	9.52 a	8.33 a	9.77 a
	Ca_1	5,140 b	5,640 b	5,490 bc	3,590 d	13.09 b	18.19 bc	20.32 b
P_1	Ca_0	4,570 a	4,920 a	5,230 ab	3,150 abc	9.45 a	8.42 a	10.57 a
	Ca_1	5,270 b	5,960 b	5,750 c	3,540 cd	14.93 c	19.87 c	23.04 c
P_2	Ca_0	4,500 a	5,050 a	4,860 a	3,100 ab	9.24 a	9.48 a	11.45 a
	Ca_1	5,270 b	5,750 b	5,970 c	3,390 bcd	14.56 c	17.41 b	22.63 c

[1] Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Multiple regression equations, describing the effect of Zn, N, P, and Ca on Ca composition by jaraguagrass, could be obtained using the model and respective coefficients given in Appendix Tables 73 and 74.

Lime, as expected, was the dominant factor in significantly increasing Ca concentrations and total uptake in both jaraguagrass forage and crown-root systems. The attributes of lime as a source of Ca and its beneficial effects on plant growth and soil environment have already been mentioned. Nitrogen became increasingly effective with each forage harvest in depressing Ca concentration while increasing total Ca uptake simultaneously. Its stimulatory effect on plant growth and nutrient absorption was a major contribution in Ca nutrition of the grass. Overtly, neither Zn nor P demonstrated any noteworthy effect on forage Ca concentrations although a significant and positive effect of Zn was observed in the third harvest. However, both Zn and P did contribute, in a minor way and in association with the other nutrients, to increase total Ca uptake by their effect on forage yield increases, especially by the third harvest.

Crown-root systems did not respond to applied Zn, N, or P with regard to Ca concentration but did significantly absorb more Ca with N_1 and N_2 treatments than control.

Calcium absorption by jaraguagrass, like P, was affected to varying degrees by all the nutrients applied. Responses were progressively more complex with each harvest such that each predicted value involved a number of interacting variables. This is not surprising since the role of lime in plant nutrition and soil fertility is diverse.

Nitrogen and Crude Protein

Nitrogen and crude protein (CP) concentrations of composite jaragua-

grass forage samples from the N and Zn treatments of each harvest are summarized in Table 31. Although these data could not be statistically analyzed, it was evident that N treatments increased forage N and CP over control in the first and second harvests. Inconsistent values were obtained from samples in the second harvest. This was attributed to sampling bias because of the small amounts of dry forage available for analyses and later harvest.

The decline in total N harvest compared to harvest in the control forage samples was clearly shown. Average N concentrations for control treatments were 0.95, 0.75, and 0.27% for the first, second, and third harvests, respectively. Mean forage values for the N_0, N_1, and N_2 treatments were 0.95, 1.31, and 1.62% N for the first harvest and 0.27, 1.36, and 1.37% N for the last harvest, respectively. Nitrogen values ranged from 0.06 to 1.74% N and CP values from 0.38 to 10.88%. These values were comparable or higher than those reported for jaraguagrass by Blue et al. (23) in eastern Panama, and Blue (22) and Tergas (243) in Costa Rica. These relatively high N or CP values for jaraguagrass forage were not surprising since total N applied for the entire experiment was equivalent to 150 and 300 kg N/ha as urea spray. The N_2 treatment by the third harvest increased forage N and CP concentrations. For sustained high quality herbage in an intensive pasture system N applications are essential as evidenced by the rapid decline of forage N in control plots.

Zinc did not show any appreciable effect on forage N or CP concentration values.

Other Elemental Concentrations

Main effects of applied nutrients on elemental concentrations of

Table 31. Effect of applied N and Zn on N and crude protein[1] concentra-
tions of jaraguagrass forage.

Treatment[2]		Total N Harvest			Crude protein Harvest		
		1	2	3	1	2	3
		---------- % ----------			---------- % ----------		
N_0	Zn_0	0.90	0.69	0.10	5.63	4.31	0.63
	Zn_1	0.95	0.77	0.06	5.94	4.81	0.38
	Zn_2	0.99	0.78	0.66	6.19	4.88	4.13
N_1	Zn_0	1.33	0.14	1.53	8.31	0.88	9.56
	Zn_1	1.32	0.98	1.23	8.25	6.13	7.69
	Zn_2	1.28	1.46	1.32	8.00	9.13	8.25
N_2	Zn_0	1.56	0.57	1.32	9.75	3.56	8.25
	Zn_1	1.74	0.84	1.42	10.88	5.25	8.88
	Zn_2	1.55	0.35	1.38	9.69	2.19	8.63

[1]Nitrogen concentration x 6.25 (114).

[2]Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha;
and Zn_0, Zn_1 and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

Mg, Fe, Cu, Mn, and Sr in jaraguagrass forage are summarized in Appendix
Table 75. Forage Mn concentrations were notably lower with all applied
fertilizer treatments in the first harvest and Fe concentrations ap-
peared to be higher with N_2 treatment over control. No consistent
response trends were observed for other elemental values.

Soil pH and Extractable Nutrients

Soil pH values ranged from 5.21 to 6.45 and 4.04 to 5.17 for pH
measured in soil:water and soil:KCl suspensions, respectively. Extract-
able Zn varied from 0.1 to 3.6 ppm while extractable P and Ca ranged
from trace to 59.5 and 2,850 to 5,780 ppm, respectively.

Main treatments effects

Main effects of applied nutrients on soil pH and extractable Zn,
P, and Ca from the jaraguagrass pot experiment are summarized in Table
32.

Soil pH.--As expected, lime application significantly (P = 0.01)
increased average soil pH values over control from 5.43 to 6.17 and
4.15 to 4.99 for water- and KCl-soil suspension measurements, respec-
tively (Fig. 28). The increase of 0.74 - 0.84 pH units with liming
was considered quite appreciable for Santa Fe soils which measured the
highest titratable exchange acidity (21.1 meq/100 g) in comparison
with other major eastern Panamanian soils (188). Analysis of the
Santa Fe surface soils revealed relatively high contents of organic
matter, amorphous material, and interstratified mixtures of montmoril-
lonite, vermiculite, and illite clay minerals which were indicative
of the high buffering capacity of these soils. Relative to other major
Panamanian soils studied, Reneau (188) also found that Santa Fe soils
had the highest pH-dependent charge capacity of 14.8 meq/100 g. The

Table 32. Main effects of applied Zn, N, P, and Ca on soil pH and extractable Zn, P, and Ca from jaraguagrass pot experiment.

Treatment[1]	pH		Extractable nutrients		
	(H_2O)	(KCl)	Zn	P	Ca
			--------------- ppm ---------------		
Zn_0	5.81 a[2]	4.57 a	0.58 a	26.9 a	4,270 a
Zn_1	5.81 a	4.57 a	0.80 b	25.3 a	4,240 a
Zn_2	5.79 a	4.57 a	0.91 b	25.5 a	4,290 a
N_0	5.79 a	4.61 b	0.78 a	23.6 a	4,260 ab
N_1	5.81 a	4.55 a	0.74 a	27.0 a	4,220 a
N_2	5.81 a	4.55 a	0.77 a	27.1 a	4,320 b
P_0	5.79 a	4.57 a	0.76 a	16.1 a	4,210 a
P_1	5.80 a	4.56 a	0.79 a	26.3 b	4,260 ab
P_2	5.81 a	4.57 a	0.73 a	35.2 c	4,300 b
Ca_0	5.43 a	4.15 a	0.90 b	30.6 b	3,320 a
Ca_1	6.17 b	4.99 b	0.62 a	21.2 a	5,210 b

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; N_0, N_1 and N_2 to 0, 50, and 100 kg N/ha; P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.
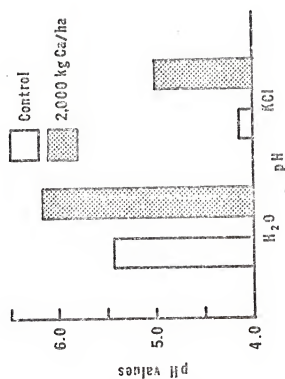
Fig. 28. Relationship between applied Ca and soil pH values of jaraguagrass pot experiment soil.

difference between pH (H_2O) and pH (KCl) measurements of 0.72 and 1.18 pH units for control and lime treatments, respectively, also indicated the relatively high amounts of Al^{+++} and H^+ ions which have been dissociated from the soil colloidal exchange sites by K^+ ions. Soil pH measured in N̲ KCl is generally considered to reflect the intrinsic characteristics of the soil since the value is less influenced by biological or meteorological changes in the soil environment. Liming the Santa Fe soils therefore increased pH-dependent charges and base saturation by dissociation of the H^+, complex Al^{+++} and Fe^{++} ions from the colloidal exchange sites.

Analysis of variance showed that a N x P interaction for pH (H_2O) and N levels for pH (KCl) were significant ($P = 0.01$). However, main effects of Zn, N, and P on soil pH (H_2O) were not significant and Zn and P did not affect soil pH (KCl). Nitrogen treatments significantly decreased soil pH (KCl) from control while showing a trend of increasing soil pH (H_2O). The differences under discussion were only 0.08 pH units or less which, from a practical point of view are insignificant.

Soil Zn.--Although the differences in response were not significant between Zn_1 and Zn_2, both treatments significantly ($P = 0.01$) increased extractable Zn over control by 37 and 57%, respectively (Fig. 29). These extraction values of 0.58 - 0.91 ppm Zn are considered low but it must be borne in mind that the pot soils were sampled after three forage harvests. In addition, the extraction solution was buffered at pH 7 and thus would extract less Zn than actually available at pH (H_2O) 5.21 to 6.45 of the sampled soil. In general, availability of Zn decreased with increase in soil pH. With the exception of the first forage harvest, Zn concentration and total uptake values of jaraguagrass
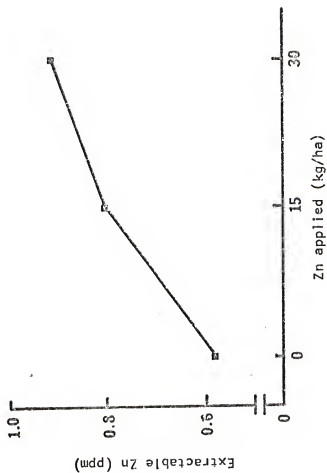
Fig. 29. Relationship between applied Zn and extractable Zn from jaraguagrass pot experiment soil.

were relatively high and significantly increased by applied Zn in this study. The implications are that availability of soil Zn was higher than measured and that jaraguagrass root systems may have also been efficient in absorbing Zn from the soil. Besides crop removal, applied Zn may have been adsorbed to organic or inorganic soil surfaces, precipitated with other soil components such as Ca, Al and Fe, incorporated in biological systems and their residues, and occupied sites in soil minerals by entering the crystal lattice through solid state diffusion. Although Zn was applied in solution, the nature of the Santa Fe soil with its high contents of OM and amorphous and interlayered montmorillonitic clays makes loss by leaching unlikely.

Lime significantly ($P = 0.01$) decreased extractable Zn by approximately 30%. Many workers have reported the decrease in available Zn or plant Zn uptake with liming (28, 154, 198, 213, 214, 271, 290). The effect of lime is essentially associated with the concomitant increase in soil pH. Extractable Zn in this study was inversely related to soil pH which was in agreement with other investigators (12, 17, 122, 139, 154, 198) some of whom also observed that most pH-induced deficiencies occurred within the range of pH 6.0 to 8.0.

In addition to the pH effect of lime applications, $CaCO_3$ may act as a strong adsorbent for Zn (121, 164). This effect is highly probable in this study since $CaCO_3$ was applied and thoroughly mixed with the soil in a powder form which had a high reactive surface area. In this way lime may have decreased mobility of Zn in the soil.

Neither N nor P showed any significant effect on extractable Zn individually but a N x P interaction was found significant ($P = 0.05$).

Soil P.--Significant ($P = 0.01$) increases in extractable P were

recorded with P fertilizer applications. The increases over control were by 45 and 120% for P_1 and P_2 rates, respectively (Fig. 30). Mean extractable P value of 16.1 ppm P for control was considered low, but the 25.3 and 35.2 ppm extractable P for P_1 and P_2 treatments, respectively, were high. Acid-soluble forms of P, largely Ca phosphates and a proportion of Al and Fe phosphates, were extracted by the NH_4F/HCl method used (172). Lime significantly ($P = 0.01$) depressed extractable P in the soil by about 30% from control. Although application of lime raises soil pH to a range where the maximum amount of plant-available $HPO_4^=$ and $H_2PO_4^-$ ionic forms are present, applied P may still be immobilized by adsorption to exposed colloidal surfaces containing Fe and Al, formation of compounds of low solubility with Ca or Mg and chemical precipitation with Al and Fe inside or outside the root systems. In addition, phosphates may be adsorbed on lime particles.

Zinc and N levels did not significantly affect extractable P although N did show a trend in increasing P availability.

Soil Ca.--Lime increased extractable Ca significantly ($P = 0.01$) and by over 57%. Both N_2 and P_2 rates showed significant positive effects in increasing extractable Ca although the actual differences of 120 and 60 ppm Ca, respectively, may be considered relatively small. This aspect will be discussed further under the appropiate interaction sections. Zinc had no effect on extractable Ca.

Zn x N

Effect of applied Zn and N on soil pH and extractable nutrients is shown in Table 33.

Soil pH.--Zinc and N treatments did not affect pH (H_2O) values although an incipient effect of N in increasing pH values was observed
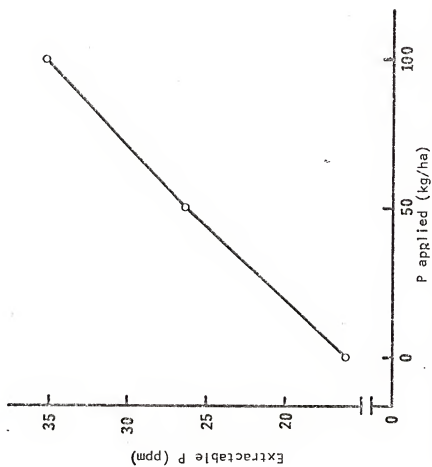
Fig. 30. Relationship between applied P and extractable P from jaraguagrass pot experiment soil.

Table 33. Effect of applied Zn and N on soil pH and extractable Zn, P and Ca from jaraguagrass pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				------------- ppm -------------		
Zn_0	N_0	5.79 a[2]	4.61 c	0.58 a	22.6 a	4,250 ab
	N_1	5.83 a	4.54 a	0.49 a	28.1 a	4,220 ab
	N_2	5.80 a	4.56 ab	0.66 abc	30.0 b	4,330 ab
Zn_1	N_0	5.79 a	4.59 bc	0.84 bc	23.7 a	4,240 ab
	N_1	5.82 a	4.56 ab	0.82 bc	25.3 a	4,200 a
	N_2	5.80 a	4.55 ab	0.73 abc	26.8 a	4,280 ab
Zn_2	N_0	5.79 a	4.62 c	0.92 c	24.6 a	4,280 ab
	N_1	5.77 a	4.54 a	0.89 c	27.5 a	4,230 ab
	N_2	5.82 a	4.55 ab	0.91 c	24.4 a	4,360 b

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; and N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

and associated with a significant N x P interaction. Nitrogen, irre-
spective of Zn levels, however, significantly decreased soil pH (KCl)
from control. It is conceivable that, since N applications were
relatively high, rapid hydrolysis of urea to NH_4 ions followed by
nitrification to NO_3 ions could lead to potential acidity. Ammonium
ions could also be adsorbed on the colloidal exchange complex by re-
placing bases which upon leaching would also lower soil pH indirectly.

Soil Zn.--Zinc had an overriding effect over N in increasing
extractable Zn but N showed an incipient (with P) depressing effect
especially for treatments N_1Zn_0 and N_2Zn_1 (Fig. 31). The implications
will be discussed later.

Soil P and Ca.--Nitrogen and Zn showed no consistent effect on
extractable P or Ca.

P x Zn

Table 34 describes the effect of applied P and Zn on soil pH and
extractable nutrients.

Soil pH.--Neither P nor Zn had any overt effect on soil reactions.

Soil Zn.--Although Zn applications increased extractable Zn its
effect was reduced by a negative influence of increasing rates of P
(Fig. 31). The effect of P was closely associated with a N x P inter-
action which will be discussed later.

Soil P and Ca.--Phosphorus increased extractable P significantly
irrespective of Zn levels. Extractable Ca levels were not significantly
different with P and Zn applications.

Ca x Zn

Data given in Table 35 illustrate the effect of Ca and Zn on soil
reaction and extractable nutrients.
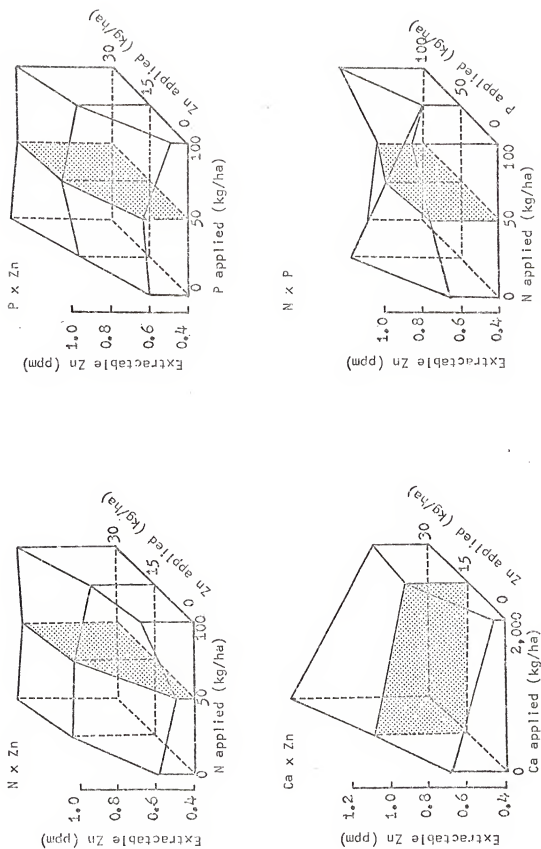
Fig. 31. Relationship between applied nutrients on extractable Zn from jaraguagrass pot experiment soil.

Table 34. Effect of applied P and Zn on soil pH and extractable Zn, P, and Ca from jaraguagrass pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				---------- ppm ----------		
P_0	Zn_0	5.79 a[2]	4.57 a	0.60 ab	16.6 a	4,200 a
	Zn_1	5.79 a	4.57 a	0.76 abcd	15.8 a	4,170 a
	Zn_2	5.77 a	4.57 a	0.93 d	15.9 a	4,270 a
P_1	Zn_0	5.80 a	4.56 a	0.63 abc	25.9 b	4,260 a
	Zn_1	5.83 a	4.57 a	0.86 bcd	26.7 b	4,270 a
	Zn_2	5.78 a	4.56 a	0.89 cd	26.3 b	4,240 a
P_2	Zn_0	5.82 a	4.58 a	0.49 a	38.1 c	4,340 a
	Zn_1	5.79 a	4.56 a	0.78 bcd	33.3 c	4,280 a
	Zn_2	5.83 a	4.58 a	0.90 cd	34.2 c	4,360 a

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 35. Effect of applied Ca and Zn on soil pH and extractable Zn,
          P, and Ca from jaraguagrass pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				------------- ppm -------------		
Ca_0	Zn_0	5.43 a[2]	4.16 a	0.69 b	30.5 c	3,330 a
	Zn_1	5.45 a	4.15 a	0.89 b	31.5 c	3,310 a
	Zn_2	5.41 a	4.15 a	1.12 c	29.7 c	3,320 a
Ca_1	Zn_0	6.18 b	4.98 b	0.46 a	23.2 b	5,210 b
	Zn_1	6.16 b	4.99 b	0.71 b	19.1 a	5,170 b
	Zn_2	6.18 b	5.00 b	0.69 b	21.3 ab	5,260 b

[1]Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and
Zn_0, Zn_1 and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

Soil pH.--Calcium significantly increased soil pH over control
with no effect from applied Zn.

Soil Zn.--In the absence of lime, Zn increased extractable Zn
over control. However, only the Zn_2 rate was significantly different
from both Zn_1 and control. Addition of lime had a profound effect on
depressing extractable Zn such that values were statistically equiva-
lent to control (Fig. 31). Lime resulted in a low extractable Zn
value of 0.46 ppm when no Zn was applied.

Soil P and Ca.--Lime was dominant in decreasing extractable P
and increasing Ca irrespective of Zn levels.

N x P

Table 36 shows the effect of N and P amendments on soil reaction
and extractable nutrients.

Soil pH.--From the analysis of variance (Appendix Table 72), a
N x P interaction (P = 0.01) was observed on soil pH (H_2O). The effect
was essentially at the N_2 rate where increasing rates of applied P
resulted in a concomitant increase in soil pH by 0.08 units. It was
also interesting to note that extractable Ca was significantly in-
creased at the same N x P rates which probably accounted for the slight
rise in pH (H_2O). However, N_1 and N_2 treatments significantly decreased
soil ph (KCl) over N_0 treatment irrespective of P levels. Significant
differences were only 0.05 to 0.07 pH units and, practically, may be
regarded as insignificant. The theoretical implication is that applied
N increased exchange acidity. Rapid hydrolysis of urea followed by
intrification probably resulted in acidification of the soil environment.

Soil Zn.--Figure 31 illustrates the N x P interaction (P = 0.05)
on extractable Zn. In the absence of P, N applications showed a

Table 36. Effect of applied N and P on soil pH and extractable Zn, P, and Ca from jaraguagrass pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				-------------- ppm --------------		
N_0	P_0	5.77 ab[2]	4.62 c	0.67 a	14.0 a	4,270 ab
	P_1	5.77 ab	4.61 bc	0.98 b	25.9 bc	4,240 a
	P_2	5.83 ab	4.61 bc	0.69 ab	31.0 cd	4,260 ab
N_1	P_0	5.83 ab	4.56 a	0.76 ab	14.6 a	4,180 a
	P_1	5.82 ab	4.54 a	0.80 ab	26.3 bc	4,200 a
	P_2	5.77 ab	4.55 a	0.64 a	40.0 e	4,280 ab
N_2	P_0	5.76 a	4.54 a	0.86 ab	19.8 ab	4,190 a
	P_1	5.82 ab	4.54 a	0.60 a	26.7 bc	4,330 ab
	P_2	5.84 b	4.57 ab	0.84 ab	34.7 de	4,440 b

[1] Treatments N_0, N_1, and N_2 were equivalent to 0, 50, and 100 kg N/ha; and P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

positive trend in increasing extractable Zn. However, at the P_1 rate, no consistent effect was observed. Although some significant differences were noticeable between means, Zn extractable values were relatively small. The N x P interaction may involve complex ion formation with Zn, Ca, Al- and Fe-hydroxy, and other ions. In the absence of P, applied N may have increased extractable Zn through its localized effect on lowering soil pH in the manner discussed earlier. Application of N with increments of P may have decreased extractable Zn through complex ion formation involving possibly NH_4, PO_4, Zn, Ca, Al- and Fe-hydroxy, and other ions. Zinc has been found to form stable complex ions or compounds with NH_4^+ (246) $P_4^=$, (48, 54, 81, 124, 207) or both to give reaction products such as $ZnNH_4PO_4$ (161). These compounds may also be adsorbed on soil colloidal exchange sites.

Soil P and Ca.--Applied P had an overriding effect in increasing extractable P but a positive incipient effect of N x P interaction was noted. Extractable Ca was increased at the N_1 and N_2 treatment levels with increments of P. It may be pertinent to note that the P treatments were applied as monocalcium phosphate which could be a direct source of available Ca ions. Indirectly, upon absorption of water, monocalcium phosphate is a source of H_3PO_4 which may contribute to extractable Ca through various intermediate compounds as a result of chemical interactions in the soil.

N x Ca

The data presented in Table 37 show the effect of applied N and Ca on soil reaction and extractable nutrients.

Soil pH.--Lime was dominant over N in significantly increasing soil pH although the effects of N in raising pH (H_2O) and decreasing pH (KCl) were noticed.

Table 37. Effect of applied N and Ca on soil pH and extractable Zn, P, and Ca from jaraguagrass pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				------------- ppm -------------		
N_0	Ca_0	5.41 a[2]	4.19 a	0.89 bc	27.7 bc	3,340 a
	Ca_1	6.17 b	5.03 b	0.68 ab	19.6 a	5,170 b
N_1	Ca_0	5.44 a	4.13 a	0.92 c	31.6 c	3,300 a
	Ca_1	6.17 b	4.97 b	0.55 a	23.3 ab	5,140 b
N_2	Ca_0	5.44 a	4.14 a	0.90 bc	32.5 c	3,320 a
	Ca_1	6.17 b	4.96 b	0.64 a	21.6 a	5,320 b

[1]Treatments N_0, N_1, and N_2 were equivalent to 0, 50 and 100 kg N/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Soil Zn.--Extractable Zn was significantly depressed by liming irrespective of applied N. The noticeable low value for N_1Ca_1 treatment of 0.55 ppm extractable Zn was caused by the N x P interaction mentioned earlier.

Soil P and Ca.--Again lime was instrumental in decreasing extractable P and increasing extractable Ca. Increments of N had a minor effect in ameliorating the depressing effect of lime on soil P and in enhancing the availability of soil Ca.

P x Ca

Phosphorus and Ca applications and their effect on soil reaction and extractable nutrients are given in Table 38.

Soil pH.--Irrespective of P, lime significantly elevated soil pH over control.

Soil Zn.--Lime significantly decreased extractable Zn but its effect was mollified by the P_1 treatment such that the difference between limed and unlimed soil was not significant. This was again attributed to N x P interaction.

Soil P and Ca.--Phosphorus significantly increased extractable P in the absence of lime but lime significantly lowered these values such that only P_1 and P_2 treatments increased soil P over P_0Ca_0 treatment. Extractable Ca, as expected, was significantly increased by liming. A modest enhancement effect was observed with the P_1 and P_2 treatments over control.

Equations for Soil Reaction and Extractable Nutrients

Multiple regression equations for soil reaction and extractable Zn, P, and Ca from jaraguagrass pot experiment soils are given below for general reference. Calculations were made using the regression

Table 38. Effect of applied P and Ca on soil pH and extractable Zn, P and Ca from jaraguagrass pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				ppm		
P_0	Ca_0	5.41 a[2]	4.16 a	0.90 c	19.8 b	3,280 a
	Ca_1	6.16 b	4.99 b	0.63 ab	12.4 a	5,150 b
P_1	Ca_0	5.43 a	4.14 a	0.85 bc	29.7 d	3,270 a
	Ca_1	6.17 b	4.98 b	0.74 bc	22.9 bc	5,240 b
P_2	Ca_0	5.44 a	4.16 a	0.96 c	42.2 e	3,410 a
	Ca_1	6.19 b	4.99 b	0.50 a	28.3 cd	5,240 b

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

model and coded treatment variables in Appendix Table 73 and coeffi-
cients presented in Appendix Table 74. The equations are as follows:

$$\text{Soil pH } (H_2O) = 5.80 + 0.008x_3 - 0.002x_4 + 0.015x_5 - 0.001x_6$$
$$+ 0.370x_7 + 0.004x_3x_5 - 0.007x_3x_6$$
$$+ 0.023x_4x_5 \qquad [8]$$

$$\text{Soil pH (KCl)} = 4.57 - 0.029x_3 + 0.01x_4 + 0.417x_7 \qquad [9]$$

$$\text{Soil Zn} = 0.76 + 0.166x_1 - 0.007x_3 - 0.018x_5 - 0.017x_6$$
$$- 0.14x_7 - 0.013x_3x_5 - 0.092x_3x_6 \qquad [10]$$

$$\text{Soil P} = 25.9 + 1.71x_3 - 0.54x_4 + 9.56x_5 - 0.21x_6$$
$$- 4.7x_7 - 0.51x_3x_5 + 0.65x_3x_6$$
$$- 1.57x_4x_5 \qquad [11]$$

$$\text{Soil Ca} = 4,265 + 32x_3 + 57x_5 + 945x_7 + 69x_3x_5 \qquad [12]$$

where Soil pH (H_2O) and pH (KCl) are pH values for readings taken in
2:1 soil:water and soil:KCl suspensions, respectively; Soil Zn, P, and
Ca are extractable Zn, P, and Ca in ppm of air-dry soil, respectively;
and x_1, x_3, x_4, x_5, x_6, x_7 refer to coded treatment variables Zn (linear),
N (linear), N (quadratic), P (linear), P (quadratic) and Ca (linear)
in kg/ha, respectively.

In summary, lime was the dominant factor in its effect on soil
responses. Lime significantly increased soil pH by between 0.74 to
0.84 pH units, and, essentially through its effect on soil pH, decreased
both soil extractable Zn and P by 30%, and increased extractable Ca
by over 57%. The direct effect of lime, applied in the form of finely
divided powder, as an adsorbent for soil Zn and P was also deemed an

important factor in reduction of these extractable nutrients. Other
direct and indirect roles of lime on soil chemistry and fertility
previously discussed were no doubt relevant to the soil responses
obtained.

Zinc applications significantly increased extractable Zn over
control by between 37 to 57% but the mean values of 0.80 and 0.91 ppm
Zn were considered relatively low. These low values were partly at-
tributed to the use of $1\underline{N}$ NH_4OAc buffered at pH 7 to extract soil Zn
when the actual soil pH values were considerably lower. Zinc had no
appreciable effect on soil reaction or extractable P and Ca.

Addition of P_1 and P_2 rates significantly increased NH_4F/HCl ex-
tractable P over control by 12 and 45%, respectively. These extraction
values over control suggested that P was highly available (172). Phos-
phorus had no direct effect on soil reaction or extractable Zn and Ca.

A significant effect of N applications on decreasing soil (KCl) by
about 0.08 pH units was observed. From a practical point of view this
difference may not be significant although a theoretical reason for
this response was ventured. Upon further investigation, it appeared
that N x P interactions had a dominant influence on soil pH (H_2O) and
extractable Zn and an incipient effect on extractable Ca. The effect
of N applied in solution as urea and the subsequent hydrolysis to NH_4
ions and possible nitrification to NO_3 ions may have been the underlying
cause to subsequent soil reactions. Possible complex ion formation and
exchange reactions involving NH_4, Zn, Ca, and Al, Fe-hydroxy ions and
their association with the mineral and organic soil colloids were in-
volved in relation to the responses measured. Examination of the
multiple regression equations for soil responses indicates the complexity
of predictive evaluation of soil reactions.

Soil Nitrogen

Average values of total soil N were 0.41, 0.40, and 0.39% for composite samples of N_0, N_1, and N_2 treates soils, respectively. Soils which received the full fertilizer complement (N_2, P_2, Zn_2, and Ca_1) gave a mean value of 0.37% total N. These values are considered high relative to those reported by Gamble et al. (80) for Santa Fe soils. The effect of higher jaraguagrass yields as a result of N and other fertilizer amendments appear to have lowered the soil N reserves. Nitrogen fixation, in the form of NH_4^+, was considered probable because of the high proportion of interlayered 2:1 type structured clays and organic matter in the Santa Fe surface soils. This would account for the moderately high soil N values obtained.

Comparison Between Control and Fertilized Jaraguagrass

Data presented in Appendix Table 76 show the comparison of yields and elemental composition between control and fertilized (N_2, P_2, Zn_2 and Ca_1 treatment) jaraguagrass. Full fertilizer treatment had a dramatic effect on increasing jaraguagrass yields, Zn concentrations, and total Zn, P, and Ca uptake. Forage P and Ca concentrations were almost equal to or lower than control values due to the dilution effect of substantially higher yields. Forage yields of fertilized jaraguagrass were 200 to 500% higher than control for the three forage harvests while mean crown-root yield was over 170% higher than control. Zinc concentrations of fertilized forage and crown-root systems were 120 to 150% higher than control. However, total Zn uptake by forage was 260 to 600% higher for the three harvests and almost 300% higher by crown-root systems. These data illustrate the tremendous capacity of jaraguagrass (especially the crown-root system) to absorb and accumulate Zn and other added nutrients.

Effect of Jaraguagrass and Fertilizer on Pot Soils

A comparison of soil reaction and extractable nutrients was made
between untreated (prior to experiment), control, and fertilized (N_2,
P_2, Zn_2, and Ca treatment) soils from jaraguagrass pot experiment.
Cropping without complete fertilizer treatment (control) resulted in
a slight decrease in soil pH (0.07-0.1 pH units for H_2O and KCl read-
ings, respectively) and decrease of extractable Zn and Ca by 64 and
31%, respectively, compared to untreated soil. Cropping with complete
fertilizer however increased soil pH by 0.90 (H_2O) and 1.30 (KCl) pH
units, and extractable Ca by 16% over untreated soil. However, ex-
tractable Zn of 0.6 ppm was 76% lower than untreated soil. Since
addition of lime affected soil pH the Zn reserves were probably much
higher. Extractable P values were comparable in all three soils.
Phosphorus reserves in the control soil evidently supplied jaraguagrass
and maintained extractable P close to the untreated soil value. These
results indicated that intensive cultivation with crop removal, even
over a short period of time, rapidly drained soil reserves and reduced
crop yields.

Nutrient Recovery

A balance sheet of nutrients applied and nutrients recovered gives
some additional information regarding the relative absorptive efficiency
of the plant rooting system and nutrient supplying or fixing capacity
of the soil. It is difficult in a multivariate study to calculate
precise nutrient recoveries since the control value for main treatment
effects is generally inflated with other applied nutrient interactions.
However, an attempt has been made to estimate recoveries of an applied
nutrient by subtracting total nutrient uptake of unfertilized jaragua-

grass tissues (which have not received any of the fertilizer nutrients studied) from the total nutrient uptake measured for a specific treatment level. These estimates are subject to gross errors and are essentially for comparative evaluations.

Calculated nutrient recoveries of applied Zn, P, and Ca from the jaraguagrass pot experiment are presented in Appendix Table 78. In general, nutrient recovery values by jaraguagrass were low. Zinc recoveries by forage and crown-root systems were estimated to be 0.65 and 2.04% for Zn_1 treatment rate and 0.43 and 2.12% for Zn_2, respectively. Forage Zn recoveries were 68 and 80% lower than for crown-root systems in the Zn_1 and Zn_2 treatments, respectively. There was an indication that increasing applications from Zn_1 to Zn_2 rates resulted in Zn accumulation in crown-root systems relative to forage uptake. Recovery of Zn applied at Zn_1 rate by the whole plant was slightly higher (0.14%) compared to the Zn_2 treatment. Over 97% of the applied Zn seemed to have remained in the soil compartment. This estimate includes a negligible amount of Zn lost by leaching; adsorbed, immobilized, or fixed by soil colloids and organic material; and available Zn. Estimated extractable Zn values were roughly 2.0 to 1.5% of the amount applied.

Phosphorus recoveries by jaraguagrass forage and crown-root systems were calculated to be 5.21 and 2.61% for P_1 rate, and 5.40 and 2.78% for P_2 rate, respectively. Forage P recoveries were approximately twice that of crown-root systems. Total plant P recovery was 3.37% higher at the P_1 rate than the P_2 rate. About 92 to 95% of applied P remained in the soil compartment. Estimated available P in the soil compartment from NH_4F/HCl extractable P values was about 24% of applied P.

Recoveries of applied Ca by forage and crown-root systems were only 0.82 and 0.65%, respectively. Estimated plant available Ca from mean extractable Ca value was about 8% higher than Ca applied as lime. This reflects the effect of lime on increasing availability of basic cations.

Nitrogen recoveries by jaraguagrass forage were not included in Appendix Table 78 because of incomplete data. However, estimated forage recoveries for the first harvest were 18% for the N_1 rate and 15% for the N_2 rate. By the third harvest, forage N recoveries were 56 and 28% for N_1 and N_2 rates, respectively. Recoveries of fertilizer N from growing crops generally average about 50% (144). It was apparent that much of the fertilizer N applied at the N_2 rate was immobilized or lost through leaching and volatilization.

Hairy Indigo Pot Experiment

Elemental concentrations of crowns and roots of hairy indigo have been corrected for soil contamination which ranged from 0.02 to 13.34% of the oven-dry sample. In general, soil contamination for the legume crown-root systems was approximately one-half that reported earlier for jaraguagrass. Yields and total nutrient uptake values for crown-root systems of hairy indigo were not corrected for soil contamination. Nutrient uptake values by crown-root systems have been presented in tables showing the main treatment effects only.

Since hairy indigo and jaraguagrass were grown in the same soil type, under the same environmental conditions, and for similar periods, comparisons between treatment responses have been made. Summaries of F tests from the analysis of variance on hairy indigo and soil data are shown in Appendix Tables 79 and 80, respectively.

Multiple Regression Model and Coefficients

A multiple regression model for the hairy indigo pot experiment is presented in Appendix Table 81 and corresponding constants and regression coefficients in Appendix Table 82. All treatment responses and their constants have been listed in Appendix Table 82, regardless of significant treatment effects.

Yields

Oven-dry yields of hairy indigo ranged from 1.86 to 3.68, 2.14 to 6.21, 0.87 to 4.24, and 1.12 to 2.86 g/pot for the first, second, and third forage harvests and crown-root system, respectively. Average forage yields were 2.90, 4.03, and 2.49 g/pot (equivalent to 1,580, 2,190 and 1,360 kg/ha) for the three harvests, respectively. Mean crown-root yield was 1.70 g/pot (equivalent to 925 kg/ha).

Total hairy indigo forage yields for the three harvests were 9% higher than total jaraguagrass yields. However, average hairy indigo crown-root yield was only 18% of the jaraguagrass crown-root systems. Yield of hairy indigo crown-root systems was also 18% of the total hairy indigo forage yield whereas jaraguagrass crown-root systems exceeded total forage yield of the grass by approximately 10%. Hairy indigo forage yields declined by the third harvest while jaraguagrass forage yields generally increased from harvest to harvest. The yield decline in hairy indigo may be attributed to the shorter interval between the second and third harvests and to possible loss in vigor since the legume was an annual.

Main treatment effects

Main treatments effects of applied Zn, P, and Ca on yields of hairy indigo forage and crown-root systems are presented in Table 39.

Table 39. Main effects of applied Zn, P, and Ca on oven-dry yields of hairy indigo forage and crown-root systems.

Treatment[1]	Forage harvest			Crowns and roots
	1	2	3	
	------------------------------ g/pot ------------------------------			
Zn_0	3.03 a[2]	3.67 a	2.31 a	1.68 a
Zn_1	2.91 a	4.16 a	2.83 a	1.78 a
Zn_2	3.09 a	4.27 a	2.30 a	1.64 a
P_0	2.73 a	4.04 a	2.54 a	1.68 a
P_1	2.98 a	4.01 a	2.57 a	1.71 a
P_2	2.99 a	4.05 a	2.36 a	1.70 a
Ca_0	2.72 a	3.50 a	2.19 a	1.72 a
Ca_1	3.09 b	4.57 b	2.79 b	1.68 a

[1] Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

Response to Zn.--Yields of hairy indigo forage and crown-root systems were not significantly influenced by Zn treatments.

Response to P.--Phosphorus applications, contrary to expectation, did not significantly affect hairy indigo yields although a positive trend was observed in the first forage harvest.

Response to Ca.--Calcium, in the form of lime, significantly ($P = 0.01$) increased forage yields over unlimed treatments by 13, 31, and 27% for first, second, and third harvests, respectively (Fig. 32). Crown-root yields were not significantly affected by lime. The beneficial effects of lime on forage yields were attributed to increase in soil pH and various soil fertility factors conducive for plant growth.

P x Zn

The effects of applied P and Zn on yields of hairy indigo forage and crown-root systems (Table 40) were not statistically significant. A positive trend in yield response to P treatment was discernable for the first forage harvest.

Ca x Zn

Lime generally increased forage yields although significant differences were only observed in a few instances (Table 41). The Zn_1 treatments seemed to enhance yields in all forage harvests while Zn_2 treatment had a negative effect on yield which was especially notable in the absence of lime. Crown-root yields were increased significantly ($P = 0.05$) by Ca (linear) x Zn (linear) and Ca (linear) x Zn (quadratic) interactions. At the Zn_1 treatment rate crown-root yields were increased when lime was absent but depressed yields when lime was applied. The reverse effect was true for Zn_2 treatment rate. It would appear that
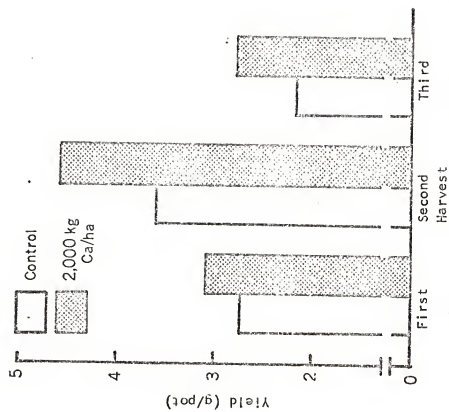
Fig. 32. Relationship between applied Ca on oven-dry yields of hairy indigo forage.

Table 40. Effect of applied P and Zn on oven-dry yields of hairy
indigo forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
				g/pot	
P_0	Zn_0	2.78 a[2]	3.28 a	2.18 a	1.62 a
	Zn_1	2.73 a	4.19 a	2.97 a	1.72 a
	Zn_2	2.70 a	4.64 a	2.49 a	1.71 a
P_1	Zn_0	2.89 a	3.83 a	2.52 a	1.68 a
	Zn_1	3.12 a	3.88 a	3.10 a	1.90 a
	Zn_2	2.93 a	4.32 a	2.09 a	1.56 a
P_2	Zn_0	2.89 a	3.89 a	2.23 a	1.74 a
	Zn_1	2.90 a	4.42 a	2.43 a	1.71 a
	Zn_2	3.19 a	3.86 a	2.42 a	1.64 a

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha;
and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

Table 41. Effect of applied Ca and Zn on oven-dry yields of hairy
indigo forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
		------------------------ g/pot ------------------------			
Ca_0	Zn_0	2.61 a[2]	3.20 a	2.10 abc	1.67 ab
	Zn_1	2.82 ab	3.91 ab	2.64 bcd	1.96 b
	Zn_2	2.72 a	3.37 ab	1.82 a	1.51 a
Ca_1	Zn_0	3.09 ab	4.13 ab	2.51 abcd	1.69 ab
	Zn_1	3.01 ab	4.41 b	3.02 d	1.59 ab
	Zn_2	3.16 b	3.50 ab	2.84 cd	1.76 ab

[1]Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and
Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

in the absence of lime the Zn_1 rate was optimum for hairy indigo crown-root yields while Zn_2 treatment had an adverse effect upon crown-root systems. When lime was added the adverse effect of the Zn_2 rate was ameliorated; presumably in decreasing availability of applied Zn in the soil.

P x Ca

Data presented in Table 42 show that P and Ca had a complementary effect on increasing forage yields in the first harvest. However, the effect of P diminished by the second forage harvest, and Ca by the third harvest. Crown-root yields were not affected by applied P or Ca.

Multiple regression equations for the relationship between applied nutrients and yield of hairy indigo forage and crown-root systems may be calculated using the regression model given in Appendix Table 80 and coefficients given in Appendix Table 81.

In summary, hairy indigo forage yields were linearly and significantly increased by lime while crown-root yields were influenced by Ca x Zn interactions in which the main effect of lime was positive and Zn was negative. Presence of nodules on harvested hairy indigo roots suggested that unknown amounts of atmospheric N had been fixed. Additionally, K was applied as a basic dressing in all treatments and may also have made an important contribution to yield increases. Applied Zn did not stimulate forage yields significantly although Zn_1 rate did show a positive trend in both forage and crown-root systems. Zinc at the Zn_2 level seemed to have had a depressing effect on hairy indigo yields in general. There is a possibility that hairy indigo roots may have been sensitive to the high level of Zn (30 kg Zn/ha). Phosphorus did not show any significant effect on legume yields. Despite

Table 42. Effect of applied P and Ca on oven-dry yields of hairy
indigo forage and crown-root systems.

Treatment[1]		Forage harvest			Crowns and roots
		1	2	3	
			g/pot		
P_0	Ca_0	2.55 a[2]	3.75 a	2.25 a	1.78 a
	Ca_1	2.92 abc	4.33 ab	2.83 a	1.58 a
P_1	Ca_0	2.81 abc	3.51 a	2.17 a	1.74 a
	Ca_1	3.14 bc	4.50 ab	2.96 a	1.69 a
P_2	Ca_0	2.78 ab	3.22 a	2.14 a	1.63 a
	Ca_1	3.20 c	4.88 b	2.59 a	1.77 a

[1]Treatments P_0, P_1 and P_2 were equivalent to 0, 50, and 100 kg P/ha;
and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

the development of a limited rooting system, hairy indigo forage yields were comparable with that of jaraguagrass.

Zinc Concentration and Total Uptake

Zinc concentration values ranged from 21 to 61, 31 to 56, 35 to 54, and 48 to 225 ppm for the three forage harvests and crown-root systems, respectively. Average forage concentration values were 36, 41, and 43 ppm Zn for the three harvests, respectively. Mean concentration of crown-root systems was 100 ppm Zn. This was over twice that of the forage concentrations. These forage Zn concentration values were much higher than for Desmodium (28 ppm Zn) sampled at Santa Fe (23).

Total Zn uptake by hairy indigo averaged 106, 163, 104, and 173 ug Zn/pot (equivalent to 0.06, 0.09, 0.06, and 0.09 kg Zn/ha) for the three forage harvests and crown-root systems, respectively.

Forage Zn concentrations of hairy indigo were over 60% higher than jaraguagrass forage in the first harvest but values for subsequent harvests were essentially the same. Total forage Zn uptake by the legume was also higher than for jaraguagrass, especially in the first two harvests when total Zn uptake was 50 to 60% higher than the grass. Crown-root Zn concentrations of hairy indigo were generally 60% that of jaraguagrass and total Zn uptake values were only 11% of the grass.

Main treatments effects

Zinc composition of hairy indigo, as affected by applied nutrients, is summarized in Table 43.

Response to Zn.--Contrary to expectations, Zn concentrations of hairy indigo forage and crown-root systems were not significantly influenced by Zn applications except in the second forage harvest when Zn values for Zn-treated plants were lower than control. This response,

Table 43. Main effects of applied Zn, P, and Ca on Zn composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake			
	Forage harvest			Crowns and roots	Forage harvest			Crowns and roots
	1	2	3		1	2	3	
	ppm				ug/pot			
Zn$_0$[2]	38 a	47 b	43 a	97 a	108 a	147 a	97 a	163 a
Zn$_1$	33 a	41 a	41 a	102 a	93 a	167 b	115 a	189 b
Zn$_2$	37 a	42 a	44 a	101 a	111 a	176 b	100 a	157 a
P$_0$	35 a	41 a	42 a	90 a	95 a	162 a	106 a	155 a
P$_1$	37 a	41 a	42 a	102 a	111 a	163 a	105 a	182 b
P$_2$	37 a	42 a	43 a	107 a	111 a	164 a	96 a	182 b
Ca$_0$	35 a	45 b	44 b	127 b	95 b	155 a	96 a	222 b
Ca$_1$	37 a	38 a	41 a	73 a	116 b	172 a	112 a	124 a

[1] Treatments Zn$_0$, Zn$_1$ and Zn$_2$ were equivalent to 0, 15, and 30 kg Zn/ha; P$_0$, P$_1$ and P$_2$ to 0, 50, and 100 kg P/ha; and Ca$_0$ and Ca$_1$ to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

which will be evident later, was due to negative effects of lime and a Ca x Zn interaction. Total Zn uptake by the forage was significantly increased in the second harvest by Zn treatments. This was due to increased forage yields. The Zn_1 treatment significantly increased total Zn uptake by crown-root systems over control and Zn_2 treatments. This was again a reflection of yields. A general increase of 5 - 9 ppm in forage Zn concentrations in hairy indigo was observed from first to the second harvest. This effect was also noticed for the jaragua-grass pot study and was attributed to mineralization of indigenous Zn in the soil and to general development of rooting systems.

Response to P.--Phosphorus treatments did not significantly affect Zn composition of hairy indigo forage at any harvest. Although Zn concentrations of crown-root systems were not significantly different, P applications significantly increased total Zn uptake over control. Since crown-root yields were similar for P treatments, there is a possibility that Zn may have been immobilized inside or on the surfaces of the rooting system. A similar observation was made in the jaragua-grass pot experiment.

Response to Ca.--Except for the first forage harvest, lime sig-nificantly reduced Zn concentrations in hairy indigo forage and crown-root systems (Fig. 33). This response was partly attributed to the negative influence of lime on Zn availability and partly to dilution effect of yield increases. Total Zn uptake by forage was only signifi-cantly increased by lime in the first harvest while crown-root Zn uptake was significantly depressed by lime. The effect of lime on increasing yields was not great enough in the last two forage harvests and crown-root harvest to offset the depressive influence on plant Zn absorption.
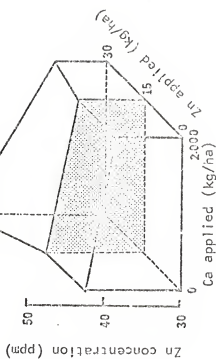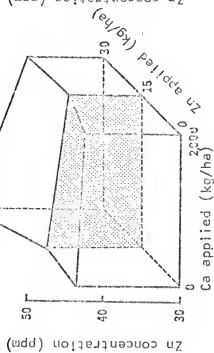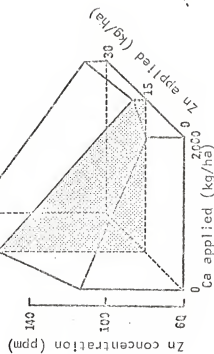
Fig. 33. Relationship between applied Ca and Zn on Zn concentrations of hairy indigo forage and crown-root systems.

P x Zn

Data presented in Table 44 show that, in general, applied P and Zn did not significantly affect hairy indigo Zn composition. The influence of P_2 treatment in ameliorating the negative effect of Zn_2 on total Zn uptake in the first forage harvest was evident and significant. Zinc may have been immobilized or fixed by phosphates in or on the roots and thus corrected the depressive effect of Zn_2 applied prior to the first harvest.

Ca x Zn

Effect of applied Ca and Zn on Zn composition of hairy indigo is shown in Table 45. Calcium (linear) x Zn (linear) interactions were found to be significant (P = 0.05) for forage Zn concentrations in the last two harvests (Fig. 34). In the absence of lime, Zn_2 forage treatment showed a positive trend in increasing forage Zn concentrations. The effect of Zn_2 was nullified when lime was added. Crown-root Zn concentrations were significantly depressed by over 50% with lime treatments irrespective of Zn applications. Total Zn uptake by forage was significantly increased by lime in the first harvest only, although an incipient positive trend could be seen in subsequent harvests. These results were again a reflection of the effect of lime in decreasing Zn availability in the soil and increasing plant yields.

P x Ca

Table 46 indicates the dominant effect of lime in depressing Zn concentrations of forage from the last two harvests and crown-root systems and in elevating total Zn uptake values in the first forage harvest. No significant response to P was noted.

Multiple regression equations for Zn concentrations in second

Table 44. Effect of applied P and Zn on Zn composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				ug/pot		
P_0 Zn_0	35 a[2]	40 a	42 a	84 a	97 ab	129 a	91 a
Zn_1	37 a	42 a	41 a	82 a	103 ab	174 a	122 a
Zn_2	32 a	40 a	43 a	105 a	86 a	184 a	105 a
P_1 Zn_0	41 a	41 a	42 a	106 a	118 ab	153 a	104 a
Zn_1	31 a	41 a	40 a	114 a	99 ab	156 a	124 a
Zn_2	40 a	42 a	45 a	85 a	117 ab	179 a	91 a
P_2 Zn_0	39 a	41 a	44 a	100 a	110 ab	157 a	95 a
Zn_1	32 a	39 a	42 a	109 a	92 ab	172 a	100 a
Zn_2	40 a	45 a	44 a	112 a	130 b	163 a	103 a

[1] Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15 and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 45. Effect of applied Ca and Zn on Zn composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				ug/pot		
Ca_0 Zn_0	38 a[2]	43 bc	43 ab	113 bc	98 a	135 a	91 ab
Zn_1	33 a	43 bc	42 a	137 c	93 a	168 ab	101 ab
Zn_2	35 a	48 c	47 b	130 c	95 a	161 ab	86 a
Ca_1 Zn_0	38 a	39 ab	42 a	80 ab	116 b	158 ab	103 ab
Zn_1	34 a	39 ab	40 a	66 a	104 ab	167 ab	119 b
Zn_2	40 a	37 a	40 a	71 a	127 b	190 b	113 ab

[1] Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.
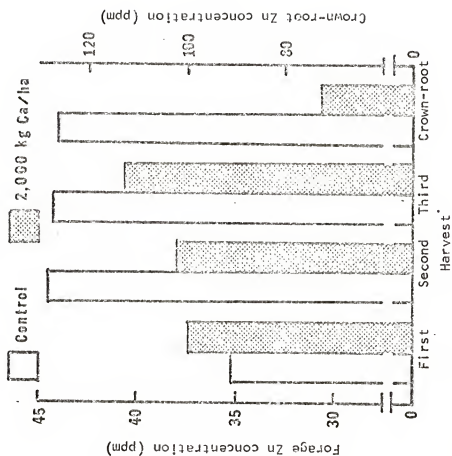
Fig. 34. Relationship between applied Ca on Zn concentrations of hairy indigo forage and crown-root systems.

Table 46. Effect of applied P and Ca on Zn composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				ug/pot		
P_0 Ca$_0$	35 a[2]	43 bc	44 ab	111 bc	89 a	161 a	98 a
Ca$_1$	35 a	38 ab	40 a	70 a	102 ab	164 a	114 a
P_1 Ca$_0$	35 a	44 c	45 b	134 c	98 ab	155 a	96 a
Ca$_1$	40 a	39 ab	40 a	70 a	125 b	171 a	116 a
P_2 Ca$_0$	36 a	46 c	45 b	135 c	99 ab	148 a	95 a
Ca$_1$	38 a	37 a	42 ab	79 ab	122 ab	161 a	105 a

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Ca$_0$ and Ca$_1$ to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

and third forage harvests and crown-root systems may be calculated using the regression model and specific coefficients in Appendix Tables 81 and 82, respectively.

In summary, lime was the major factor in affecting Zn composition of hairy indigo. The depressive effect of lime in reducing Zn concentrations in plant tissues, through its influence on decreasing available Zn, had a greater impact than stimulating total Zn uptake by increasing yields. Zinc applications demonstrated incipient positive effects by the third forage harvest and crown-root harvest. However, lime nullified these effects. Phosphorus had no significant effect on Zn composition of hairy indigo forage in general but did show an ameliorating effect on Zn_2 treatments in the first forage harvest. Phosphorus and Zn may be immobilized in the crown-root systems.

Phosphorus Concentration and Total Uptake

Phosphorus concentration values in hairy indigo ranged from 1,200 to 4,400, 825 to 4,950, 1,500 to 4,700, and 775 to 2,275 ppm for the three forage harvests and crown-root systems, respectively. Average P concentration values for the three forage harvests were 2,930, 2,560 and 2,820 ppm P, respectively. Crown-root Zn concentrations averaged 1,290 ppm P. These forage concentration values were approximately two-fold higher than those reported for hairy indigo by Bazan (18). Total P uptake by hairy indigo averaged 8.69, 10.23, 6.80, and 2.19 mg/pot (equivalent to 4.73, 5.57, 3.70, and 1.19 kg P/ha) for the three forage harvests and crown-root systems, respectively.

In comparison with jaraguagrass, hairy indigo forage and crown-root P concentration values were generally twice those recorded for the grass. Total P uptake values for hairy indigo forage were approx-

imately 370, 280, and 185% higher than jaraguagrass forage for the
three forage harvests, respectively. However, hairy indigo crown-root
total P uptake values were about 35% lower than for jaraguagrass.
This was due to the dilution effect resulting from higher crown-root
yields of the grass.

Mean treatment effects

Main treatment effects of applied nutrients on P composition of
hairy indigo are summarized in Table 47.

Response to Zn.--No significant effect of Zn levels on P composi-
tion of hairy indigo were observed.

Response to P.--Phosphorus composition of hairy indigo forage and
crown-root systems was significantly ($P = 0.01$) increased by applied
P (Figs. 35 and 36). However, differences between the P_1 and P_2 rates
were not significant for the first two forage harvests with respect to
forage P concentrations. Only the second forage harvest showed a
significant difference in total P uptake between P_1 and P_2 treatments.
However, both treatments were significantly different than control
(P_0). In general, applied P increased forage P concentrations over
control by 26 to 60%. Increases in P concentrations of crown-root
systems over control were between 18 and 42%. Similar increases over
control were recorded for total P uptake by hairy indigo.

Response to Ca.--Lime significantly ($P = 0.01$) increased P con-
centration and total uptake values by hairy indigo forage but had no
effect on crown-root systems. Beneficial effect of lime was essentially
through its effect on various soil factors that resulted in maximum
availability of P and other nutrients which in turn enhanced plant
yields. Phosphorus concentrations of forage were increased over control

Table 47. Main effects of applied Zn, P, and Ca on P composition of hairy indigo forage and crown-root systems.

	Concentration				Total uptake			
	Forage harvest			Crowns and roots	Forage harvest			Crowns and roots
Treatment[1]	1	2	3		1	2	3	
	ppm				mg/pot			
Zn_0	2,900 a[2]	2,540 a	2,900 a	1,310 a	8.40 a	9.47 a	6.46 a	2.21 a
Zn_1	2,940 a	2,650 a	2,640 a	1,330 a	8.75 a	10.92 a	7.28 a	2.35 a
Zn_2	2,940 a	2,500 a	2,930 a	1,230 a	8.93 a	10.30 a	6.65 a	2.01 a
P_0	2,140 a	1,850 a	2,240 a	1,070 a	5.93 a	7.44 a	5.65 a	1.80 a
P_1	3,250 b	2,740 b	2,820 b	1,270 b	9.78 b	10.75 b	7.09 b	2.20 ab
P_2	3,390 b	3,090 c	3,400 c	1,520 c	10.36 b	12.50 c	7.64 b	2.57 b
Ca_0	2,490 a	2,260 a	2,530 a	1,330 a	6.90 a	7.59 a	5.26 a	2.29 a
Ca_1	3,370 b	2,870 b	3,110 b	1,250 b	10.48 b	12.86 b	8.33 b	2.09 a

[1] Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15 and 30 kg Zn/ha; P_0, P_1, and P_2 to 0, 50 and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.
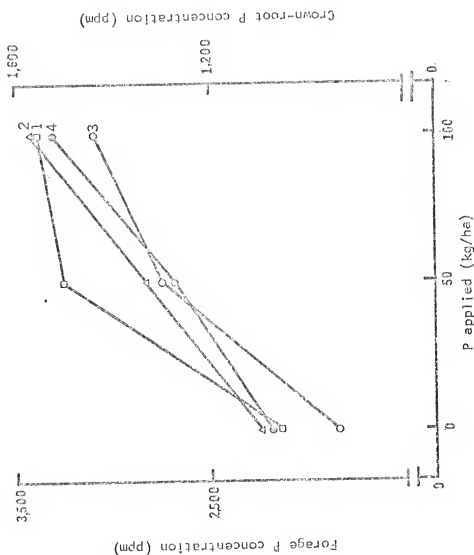
Fig. 35. Relationship between applied P on P concentrations of hairy indigo forage and crown-root systems. (Numbers 1, 2, 3, and 4 refer to first, second, and third forage harvests and crown-root harvests, respectively).
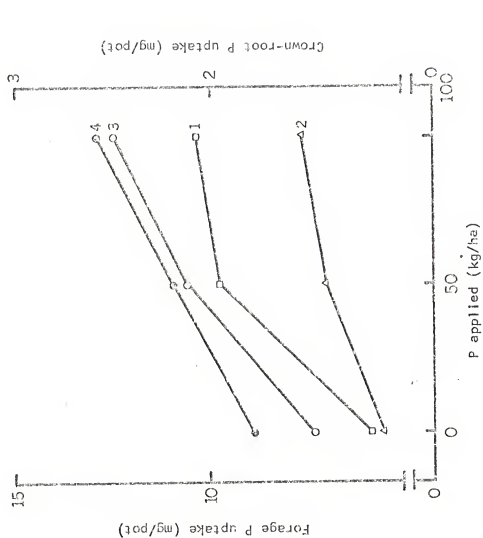
Fig. 36. Relationship between applied P on total P uptake of hairy indigo forage and crown-root systems. (Numbers, 1, 2, 3, and 4 refer to first, second, and third forage harvests and crown-root harvests, respectively).

by 43, 27 and 23% for the three forage harvests, respectively, while total P uptake values were increased over control by 51, 70, and 58%.

P x Zn

Phosphorus applications significantly increased P composition of hairy indigo forage and crown-root systems irrespective of Zn treatments (Table 48).

Ca x Zn

Lime had an overriding effect on Zn in significantly increasing P composition of hairy indigo forage for the first two harvests (Table 49). The effect of lime was neglible with respect to P concentrations of crown-root systems and did not significantly affect forage P composition by the third harvest.

P x Ca

A complementary effect of applied P and Ca on P composition of hairy indigo is demonstrated in Table 50. For the second forage harvest, a positive P (linear) x Ca (linear) interaction was found to be significant ($P = 0.05$). In general, the effect of applied P in increasing P composition of hairy indigo was greater for the first two harvests than the enhancement influence of lime. By the third harvest, lime and P were equally effective in increasing forage P compositions. Only P_2 treatments significantly increased P concentrations of the crown-root systems.

Multiple regression equations on the effect of P and Ca on P composition of hairy indigo may be formulated with reference to Appendix Tables 81 and 82.

In summary both applied P and Ca were dominant and complementary nutrient factors in increasing P composition of hairy indigo forage and

Table 48. Effect of applied P and Zn on P composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pct		
P_0							
Zn_0	2,080 a[2]	1,980 ab	2,230 ab	1,090 ab	5.89 a	6.53 a	4.87 a
Zn_1	2,150 a	1,770 a	2,150 a	1,100 ab	5.95 a	7.44 ab	6.41 ab
Zn_2	2,180 a	1,800 ab	2,340 ab	1,030 a	5.96 a	8.33 ab	5.68 ab
P_1							
Zn_0	3,170 b	2,660 bcd	3,030 bcd	1,240 ab	9.17 b	10.21 bc	7.50 b
Zn_1	3,190 b	3,150 cd	2,480 abc	1,320 abcd	10.10 b	11.74 cd	7.60 b
Zn_2	3,400 b	2,420 abc	2,940 abcd	1,270 abc	10.08 b	10.30 bc	6.17 ab
P_2							
Zn_0	3,450 b	2,980 cd	3,430 d	1,590 d	10.13 b	11.66 cd	7.02 ab
Zn_1	3,490 b	3,020 cd	3,280 cd	1,570 cd	10.19 b	13.57 d	7.82 b
Zn_2	3,240 b	3,280 d	3,500 d	1,400 bcd	10.76 b	12.27 cd	8.09 b

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15 and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 49. Effect of applied Ca and Zn on P composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pot		
Ca_0 Zn_0	2,380 a[2]	2,200 a	2,630 ab	1,350 a	6.21 a	0.70 a	0.53 a
Zn_1	2,530 a	2,220 a	2,270 a	1,360 a	7.21 a	0.85 a	0.58 a
Zn_2	2,570 a	2,340 ab	2,700 ab	1,270 a	7.28 a	0.73 a	0.47 a
Ca_1 Zn_0	3,420 b	2,880 bc	3,170 b	1,260 a	10.59 b	11.96 b	0.76 a
Zn_1	3,360 b	3,070 c	3,010 b	1,310 a	10.29 b	13.37 b	0.88 a
Zn_2	3,310 b	2,650 abc	3,150 b	1,200 a	10.58 b	13.25 b	0.86 a

[1]Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15 and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 50. Effect of applied P and Ca on P composition of hairy Indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	ppm				mg/pot		
P₀ Ca₀	1,770 a[2]	1,480 a	1,920 a	1,070 a	4.55 a	5.55 a	4.27 a
P₀ Ca₁	2,510 b	2,220 b	2,560 b	1,080 a	7.32 b	9.32 b	7.03 b
P₁ Ca₀	2,730 b	2,550 bc	2,550 ab	1,310 ab	7.73 b	8.81 b	5.20 ab
P₁ Ca₁	3,780 c	2,940 cd	3,080 bc	1,240 ab	11.84 c	12.68 c	8.98 c
P₂ Ca₀	2,980 b	2,740 bc	3,120 bc	1,600 c	8.42 b	8.42 b	6.32 b
P₂ Ca₁	3,810 a	3,450 d	3,690 c	1,440 bc	12.30 c	16.58 d	8.97 c

[1] Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

crown-root systems. Phosphorus applications had a direct effect on increasing P composition of hairy indigo while lime only increased P values of the forage, mainly through beneficial effects on plant growth and soil fertility. Zinc showed no consistent effect on P nutrition of hairy indigo.

Calcium Concentration and Total Uptake

Calcium concentration values for hairy indigo varied from 0.70 to 2.53, 1.32 to 2.18, 1.20 to 2.25, and 0.16 to 0.56% Ca for the three forage harvests and crown-root systems, respectively. Average concentration values for the three forage harvests and crown-root systems were 2.00, 1.76, 1.71, and 0.32% Ca, respectively. Bazan (18) reported a concentration range of 0.91 to 7.21% Ca in hairy indigo forage and 0.36 to 1.44% Ca in roots. Total Ca uptake by hairy indigo averaged 58.66, 72.20, 42.81, and 5.57 mg/pot (equivalent to 31.91, 39.28, 23.29, and 3.03 kg Ca/ha) for the three forage harvests and crown-root systems.

In general, Ca concentrations of hairy indigo forage were three- to four-fold higher than jaraguagrass forage. However, Ca concentrations of hairy indigo crown-root systems were similar to those recorded for jaraguagrass. For the first two forage harvests, total Ca uptake by hairy indigo was five-fold greater than by jaraguagrass forage. Despite a 60% decrease in forage yields from the second harvest, Ca uptake by hairy indigo forage was 25% higher than for the grass. Total Ca uptake by the legume for the three forage harvests was about 174 mg/pot compared to 42 mg/pot for jaraguagrass forage. The five-fold increase in crown-root yields of jaraguagrass over hairy indigo also resulted in a similar increase in total Ca uptake by the grass. It is interesting to note the higher Ca requirement and absorption by hairy

indigo compared to jaraguagrass despite similar total yields of forage
and the limited rooting system of the legume. In contrast, jaragua-
grass had a high Ca reserve in the crown-root systems.

Main treatment effects

Table 51 summarizes the effect of applied nutrients on Ca composi-
tion of hairy indigo.

Response to Zn.--Zinc did not affect Ca composition of hairy indigo
significantly.

Response to P.--Except for a significant increase in Ca concentra-
tion of crown-root system with the P_2 treatment over control, P levels
had no significant effect on hairy indigo Ca absorption. Phosphorus
and Ca may have been precipitated or adsorbed within the crown-root
system.

Response to Ca.--As expected lime significantly ($P = 0.01$) in-
creased Ca composition in hairy indigo forage but had no significant
influence on crown-root systems. Forage Ca concentrations were in-
creased over control with liming by 25, 19, and 16% for the first,
second, and third forage harvests, respectively. Total forage Ca up-
take, because of increased yields from indirect effects of lime on soil
factors, were more dramatically increased by lime. Total Ca uptake
values were 41, 57, and 51% higher than control for the three forage
harvests, respectively.

P x Zn

Table 52 shows that applied P and Zn had no consistent effect on
Ca composition of hairy indigo. A significant difference between
P_0Zn_2 treatment in increasing total forage Ca uptake over P_0Zn_0 treat-
ment was a reflection of the difference in forage yields in the second
harvest.

Table 51. Main effects of applied Zn, P and Ca composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake			
	Forage harvest			Crowns and roots	Forage harvest			Crowns and roots
	1	2	3		1	2	3	
	----- % -----				-------------- mg/pot --------------			
Zn_0[2]	1.99 a	1.74 a	1.74 a	0.33 a	57.25 a	65.41 a	40.03 a	5.64 a
Zn_1	2.03 a	1.74 a	1.67 a	0.33 a	59.45 a	72.82 a	47.42 a	5.89 a
Zn_2	1.99 a	1.81 a	1.73 a	0.31 a	59.27 a	78.36 a	40.93 a	5.17 a
P_0	1.99 a	1.72 a	1.68 a	0.30 a	54.70 a	70.34 a	42.67 a	5.08 a
P_1	2.02 a	1.80 a	1.73 a	0.31 ab	60.57 a	72.94 a	44.14 a	5.47 a
P_2	2.00 a	1.78 a	1.72 a	0.36 b	60.70 a	73.32 a	41.61 a	6.16 a
Ca_0	1.78 a	1.61 a	1.58 a	0.34 a	48.55 a	56.17 a	34.12 a	5.91a
Ca_1	2.23 b	1.92 b	1.84 b	0.31 a	68.76 b	88.23 b	51.50 b	5.23 a

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; and P_0, P_1, and P_2 to 0, 50 and 100 kg P/ha, respectively.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

Table 52. Effect of applied P and Zn on Ca composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	%				mg/pot		
P_0 Zn_0	2.00 a[2]	1.64 a	1.71 a	0.29 a	56.03 a	55.07 a	37.54 a
Zn_1	2.00 a	1.66 a	1.63 a	0.31 a	54.67 a	70.09 ab	48.24 a
Zn_2	1.98 a	1.84 a	1.70 a	0.30 a	53.41 a	85.85 b	42.24 a
P_1 Zn_0	1.95 a	1.83 a	1.85 a	0.33 a	56.78 a	71.30 ab	44.45 a
Zn_1	2.04 a	1.81 a	1.62 a	0.33 a	64.33 a	70.87 ab	50.39 a
Zn_2	2.05 a	1.75 a	1.73 a	0.28 a	60.62 a	76.66 ab	37.57 a
P_2 Zn_0	2.01 a	1.74 a	1.66 a	0.37 a	58.94 a	69.87 ab	38.09 a
Zn_1	2.05 a	1.75 a	1.76 a	0.35 a	59.35 a	77.51 ab	43.62 a
Zn_2	1.94 a	1.84 a	1.76 a	0.36 a	63.80 a	72.58 ab	43.14 a

[1] Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15 and 30 kg Zn/ha, respectively.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Ca x Zn

Lime increased forage Ca composition of hairy indigo irrespective of Zn levels but by the third harvest increasing Zn levels showed an enhancement effect on total Ca uptake (Table 53). This trend, however, was again due to the differences in forage yields. Crown-root Ca concentrations were insensitive to Ca and Zn treatments.

P x Ca

Lime was dominant over the effect of P in increasing hairy indigo forage Ca composition (Table 54). Phosphorus, at the P_2 rate, did significantly increase Ca composition of crown-root systems. This effect was caused by two unusually high values obtained from a replicate and will be assumed as experimental error.

Specific Ca concentration or total uptake values may be calculated for given levels of applied Ca by reference to Appendix Tables 81 and 82.

In summary, lime treatments significantly increased Ca concentration and total uptake values of hairy indigo forage. Neither P nor Zn showed any significant effect on the Ca nutrition of hairy indigo forage. In direct contrast to jaraguagrass,crown-root systems of the legume did not respond to lime application in any way. Phosphorus at the P_2 rate and in the absence of lime resulted in a significant increase in Ca concentration of the crown-root system over other P and Ca treatments. It was interesting to note that significant and concomitant increases in P and Zn concentrations of crown-root systems were observed for the same treatment.

Nitrogen and Crude Protein

Nitrogen and crude protein (CP) concentrations of composite hairy

Table 53. Effect of applied Ca and Zn on Ca composition of hairy indigo forage and crown-root systems.

Treatment[1]		Concentration				Total uptake		
		Forage harvest			Crowns and roots	Forage harvest		
		1	2	3		1	2	3
		%				mg/pot		
Ca_0	Zn_0	1.82 a[2]	1.61 a	1.64 ab	0.34 a	47.68 a	52.41 a	33.62 ab
	Zn_1	1.79 a	1.57 a	1.51 a	0.36 a	50.47 a	61.53 ab	39.46 abc
	Zn_2	1.73 a	1.64 a	1.61 a	0.32 a	47.50 a	54.58 a	29.29 a
Ca_1	Zn_0	2.16 b	1.86 b	1.84 bc	0.33 a	66.81 b	78.42 bc	46.43 bcd
	Zn_1	2.27 b	1.92 b	1.83 bc	0.29 a	68.43 b	84.12 bc	55.38 d
	Zn_2	2.25 b	1.98 b	1.86 c	0.31 a	71.05 b	102.15 a	52.68 cd

[1]Treatments Ca_0 and Ca_1 was equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 54. Effect of applied P and Ca on Ca composition of hairy indigo forage and crown-root systems.

Treatment[1]	Concentration				Total uptake		
	Forage harvest			Crowns and roots	Forage harvest		
	1	2	3		1	2	3
	———————— % ————————				———— mg/pot ————		
P_0 Ca_0	1.80 a[2]	1.56 a	1.59 a	0.32 a	45.81 a	58.43 a	35.91 ab
P_0 Ca_1	2.19 b	1.88 b	1.77 ab	0.28 a	63.60 b	82.25 b	49.44 bc
P_1 Ca_0	1.83 a	1.63 a	1.56 a	0.32 a	51.65 a	57.75 a	32.53 a
P_1 Ca_1	2.21 b	1.96 b	1.90 b	0.31 a	69.50 b	88.14 b	55.75 c
P_2 Ca_0	1.71 a	1.63 a	1.60 a	0.39 b	48.20 b	52.34 a	33.93 a
P_2 Ca_1	2.23 b	1.92 b	1.85 b	0.33 ab	73.20 b	94.30 b	49.30 bc

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha, and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

indigo forage samples from the Zn treatments of each harvest are summarized in Table 55. No consistent effects of Zn levels on N or CP concentrations were noticed. These values are comparable to data obtained for hairy indigo by Norris and Lawrence (169) and Wallace (269) in Florida. They reported CP values ranging from 22.6% to 10.82% depending upon stage of growth and parts of the plant. In this study values for hairy indigo ranged from 17.44 to 13.63% CP. Analysis of hairy indigo forage receiving the complete fertilizer complement (P_2, Ca_1, and Zn_2) gave CP values of 17.56, 15.56, and 16.81% for the three forage harvests, respectively.

Average concentration of actively nodulating _Desmodium_ sp. sampled at Santa Fe, eastern Panama (23) was 2.61% N (16.30% CP) which was comparable to the values shown in Table 55 for hairy indigo. The relatively high N values obtained from harvest to harvest together with visual observation of nodules on harvested roots, clearly indicated that symbiotic N fixation by rhizobia was operating efficiently in hairy indigo during the duration of the study. The value of a forage legume in fixing atmospheric N and providing quality forage in terms of high crude protein for grazing animals is clearly demonstrated. Although CP values of jaraguagrass forage from the pot study were considered high, values did not exceed 10.88% CP. In addition, N fertilizer was applied at equivalent rates of 50 - 100 kg N/ha to sustain CP percentages over 8.00% after each harvest.

Other Elemental Concentrations

Main effects of applied nutrients on elemental concentrations of Mg, Fe, Cu, Mn, and Sr in hairy indigo forage are summarized in Appendix Table 83. Forage Mg concentrations appeared to be decreased by Zn and

Table 55. Effect of applied Zn on N and crude protein[1] concentrations of hairy indigo forage.

Treatment[2]	N concentration			Crude protein		
	Harvest			Harvest		
	1	2	3	1	2	3
	---------- % ----------			---------- % ----------		
Zn_0	2.66	2.49	2.18	16.63	15.56	13.63
Zn_1	2.79	2.18	2.62	17.44	13.63	16.38
Zn_2	2.69	2.31	2.56	16.81	14.44	16.00

[1]Nitrogen concentration x 6.25 (114).

[2]Treatments were equivalent to 0, 15, and 30 kg Zn/ha.

Ca applications but increased by increments of P. Forage Fe values
were depressed by Zn levels which was in agreement with other workers
(109, 133) but increased by applied P. Lime also showed a depressing
effect on Mn and Sr concentrations of hairy indigo forage. Copper, Mn,
and Mg values of hairy indigo appear to be lower in this study than
reported elsewhere (112, 169, 269).

In comparison to elemental concentrations of jaraguagrass forage,
hairy indigo forages were generally higher in Mg and Sr by approximately
two- and four-fold, respectively, but were slightly lower in Cu and
Mn. Although Fe concentrations were generally higher in the first
hairy indigo harvest, Fe values were comparable to jaraguagrass forage
in subsequent harvests.

Soil pH and Extractable Nutrients

Soil pH values ranged from 5.03 to 5.97 and 4.00 to 5.01 for pH
measured in soil: water and soil: KCl suspensions, respectively.
Extractable Zn varied from 0.2 to 3.5 ppm Zn while extractable P and
Ca ranged from 8.1 to 52.9 ppm and 3,150 to 5,475 ppm, respectively.

In general, pH (H_2O) values were about 0.3 pH units lower for
hairy indigo pot soils than for jaraguagrass soils while pH (KCl) values
were essentially the same. The difference could be ascribed to bio-
logical or meteorological changes in the soil since pH (KCl) values
were similar.

Main treatment effects

Main treatment effects of applied nutrients on soil reaction and
extractable Zn, P, and Ca are summarized in Table 56.

Soil pH.--As expected, lime significantly (P = 0.01) increased
average soil pH values over control from 5.14 to 5.93 and 4.07 to 4.93

Table 56. Main effects of applied Zn, P, and Ca on soil pH and extractable Zn, P, and Ca from hairy indigo pot experiment.

Treatment[1]	pH		Extractable nutrients		
	(H_2O)	(KCl)	Zn	P	Ca
			---------- ppm ----------		
Zn_0	5.53 a[2]	4.53 a	0.61 a	27.8 a	4,374 a
Zn_1	5.55 a	4.49 a	0.72 a	24.9 a	4,328 a
Zn_2	5.52 a	4.49 a	0.86 a	25.7 a	4,335 a
P_0	5.53 a	4.49 a	0.71 a	17.0 a	4,271 a
P_1	5.52 a	4.49 a	0.84 a	24.2 b	4,363 b
P_2	5.54 a	4.53 a	0.63 a	37.2 c	4,403 c
Ca_0	5.14 a	4.07 a	0.90 b	28.9 b	3,354 a
Ca_1	5.93 b	4.93 b	0.55 a	23.4 a	5,337 b

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; and P_0, P_1, and P_2 to 0, 50 and 100 kg P/ha; Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

for pH (H_2O) and pH (KCl) measurements, respectively. As for jaragua-grass pot soil, an increase of 0.79 to 0.86 pH units with liming in this study was considered high for Santa Fe soils. Salient properties of this soil in relation to soil reaction discussed for the jaragua-grass study are also relevant to this section.

Neither applied Zn nor P showed any significant main effects on soil pH, although P was shown from the analysis of variance (Appendix Table 80) to significantly (P = 0.05) increase pH (KCl) values.

Soil Zn.—Contrary to expectations, application of Zn did not significantly increase soil extractable Zn despite a positive trend. A negative Ca x Zn interaction was essentially responsible for the non-significant response. This will be discussed more fully later.

Lime significantly (P = 0.01) decreased extractable Zn by approx-imately 40% (0.35 ppm Zn). The reduction was 10% greater than for jaragaugrass pot soils and may be attributed to a significant (P = 0.01) but negative Ca (linear) x Zn (linear) interaction. The effect of lime was primarily due to the concomitant increase in soil pH. As found in the jaraguagrass pot study, extractable Zn was inversely related to soil pH. In addition, lime may have further reduced Zn availability by adsorption when applied to the soil in a finely divided form.

Phosphorus showed no significant effect on extractable Zn.

Soil P.—Increments of P significantly (P = 0.01) increased extractable P over control by 42 and 120% for P_1 and P_2 treatments, respectively. These values and differences were practically the same as for the jaraguagrass pot study.

Liming significantly (P = 0.01) decreased extractable P by about 20%, which was approximately 10% less than for jaraguagrass pot soils.

The difference may be due to the fact that N fertilizer was not applied in this study as negative N x P interactions reduced P extractable values in the jaraguagrass pot soil.

Zinc applications did not affect extractable P values.

Soil Ca.--A 60% increase in extractable Ca over control was recorded significant (P = 0.01) for lime-treated soils. A similar increase was recorded for limed jaraguagrass pot soils. Application of P however also significantly (P = 0.01) increased extractable Ca although the significant differences were only 2 and 3% higher than control for P_1 and P_2 treatments, respectively. A similar increase was recorded in the jaraguagrass pot soil. It is conceivable to assume that since P was applied as Ca $H_4(PO_4)_2 \cdot H_2O$ that some of the Ca (60 and 120 mg Ca/pot for P_i and P_2 treatments) from the fertilizer might contribute to the Ca complement of the soil. In addition, $CaH_4(PO_4)_2 \cdot H_2O$ as a source of H_3PO_4 in moist soils may also dissolve and displace large quantities of absorbed Ca (plus other cations) and form hydroxyphosphate complexes. Intermediate products, such as Ca $HPO_4 \cdot 2H_2O$, may be a Ca source in the extraction procedure.

Zinc did not significantly affect extractable Ca.

P x Zn

Effect of applied P and Zn on soil reaction and extractable nutrients is shown in Table 57.

Soil pH.--Soil pH (H_2O) was not affected by P and Zn treatments but the significant effect of P in increasing pH (KCl) was observed. This may be due to the P fertilizer in reducing exchange acidity by dissociating and complexing absorbed Al, Fe, and Mn ions from the soil colloidal complex.

Table 57. Effect of applied P and Zn on soil pH and extractable Zn,
P and Ca from hairy indigo pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				-------------- ppm --------------		
P_0	Zn_0	5.52 a[2]	4.52 ab	0.47 a	19.6 ab	4,279 ab
	Zn_1	5.55 a	4.48 a	0.68 a	15.6 a	4,238 a
	Zn_2	5.53 a	4.47 a	0.98 a	15.9 a	4,296 ab
P_1	Zn_0	5.52 a	4 52 ab	1.00 a	24.0 b	4,392 bc
	Zn_1	5.55 a	4.48 a	0.68 a	24.5 b	4,371 abc
	Zn_2	5.50 a	4.47 a	0.83 a	24.1 b	4,325 abc
P_2	Zn_0	5.55 a	4.55 b	0.37 a	39.8 c	4,450 c
	Zn_1	5.57 a	4.50 ab	0.78 a	34.6 c	4,375 abc
	Zn_2	5.52 a	4.53 ab	0.75 a	37.2 c	4,383 bc

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50, and 100 kg P/ha;
and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

Soil Zn.--Neither applied P nor Zn significantly affected extractable Zn.

Soil P and Ca.--Phosphorus increments had a dominant effect over Zn in significantly increasing extractable P. Extractable Ca was increased by P although the effect appeared to be reduced by Zn applications.

Ca x Zn

Data in Table 58 show the effect of applied Ca and Zn on soil reaction and extractable nutrients.

Soil pH.--Lime generally increased soil pH irrespective of Zn levels. In the absence of lime, increments of Zn significantly decreased pH (KCl); the differences, however, were practically insignificant.

Soil Zn.--Liming significantly decreased extractable Zn but in the absence of lime, increments of Zn significantly increased extractable Zn. The Zn_2 treatment significantly increased extractable Zn over control. A negative Ca x Zn interaction and a negative Ca main effect nullified the positive effect of Zn in increasing extractable Zn.

Soil P and Ca.--Liming effectively and significantly decreased extractable P. Zinc showed a trend in decreasing extractable P, especially in the presence of lime.

P x Ca

Data in Table 59 show the influence of applied P and Ca on soil reaction and extractable nutrients.

Soil pH.--Soil pH values were significantly increased by liming. Phosphorus however significantly enhanced the effect of lime in in-

Table 58. Effect of applied Ca and Zn on soil pH and extractable Zn, P and Ca from hairy indigo pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				------------- ppm -------------		
Ca_0	Zn_0	5.14 ab[2]	4.11 b	0.58 a	30.1 b	3,367 a
	Zn_1	5.17 b	4.07 ab	0.92 ab	27.7 b	3,333 a
	Zn_2	5.11 a	4.04 a	1.21 b	28.8 b	3,361 a
Ca_1	Zn_0	5.91 c	4.94 c	0.64 a	25.5 ab	5,381 b
	Zn_1	5.94 c	4.91 c	0.51 a	22.1 a	5,322 b
	Zn_2	5.92 c	4.93 c	0.50 a	22.7 a	5,308 b

[1]Treatments Ca_0 and Ca_1 were equivalent to 0 and 2,000 kg Ca/ha; and Zn_0, Zn_1, and Zn_2 to 0, 15, and 30 kg Zn/ha, respectively.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 59. Effect of applied P and Ca on soil pH and extractable Zn,
P, and Ca from hairy indigo pot experiment.

Treatment[1]		pH		Extractable nutrients		
		(H_2O)	(KCl)	Zn	P	Ca
				------------- ppm -------------		
P_0	Ca_0	5.14 a[2]	4.07 ab	0.92 ab	19.4 b	3,289 a
	Ca_1	5.92 b	4.91 c	0.50 ab	14.6 a	5,253 d
P_1	Ca_0	5.12 a	4.04 a	0.96 c	25.8 c	3,356 bc
	Ca_1	5.92 b	4.93 c	0.72 ab	22.7 bc	5,369 e
P_2	Ca_0	5.16 a	4.11 b	0.83 ab	41.4 e	3,417 c
	Ca_1	5.93 b	4.94 c	0.43 a	32.9 d	5,389 e

[1]Treatments P_0, P_1, and P_2 were equivalent to 0, 50 and 100 kg P/ha;
and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

creasing soil pH (KCl); presumably by complexing Al- and Fe-hydroxy ions from the soil colloidal exchange sites which may then become occupied by Ca and other basic cations.

Soil Zn.--Extractable Zn was essentially decreased by liming although the P_1 treatment showed a significant increase in extractable Zn in the absence of lime and ameliorated the depressive effect of added lime.

Soil P and Ca.--Although lime had a depressing effect, increments of P still elevated extractable P values. Extractable P values ranged from a low 14.6 to a very high 41.4 ppm P. Lime had a dominant effect on increasing extractable Ca. Increments of P had a minor but significant complementary effect on increasing extractable Ca.

Equations for Soil Reaction and Extractable Nutrients

Multiple regression equations for soil reaction and extractable Zn, P, and Ca from hairy indigo pot soils were compiled for general reference using the model and coefficients given in Appendix Tables 81 and 82, respectively. The equations are as follows:

$$\text{Soil pH } (H_2O) = 5.53 + 0.393 \ z_5 \tag{13}$$

$$\text{Soil pH } (KCl) = 4.50 + 0.194 \ z_3 + 0.428 \ z_5 \tag{14}$$

$$\text{Soil Zn} = 0.73 + 0.124 \ z_1 - 0.176 \ z_5 - 0.194 \ z_1 z_5 \tag{15}$$

$$\text{Soil P} = 26.1 + 10.08 \ z_3 + 0.96 \ z_4 - 2.72 \ z_5 \tag{16}$$

$$\text{Soil Ca} = 4.345 + 66 \ z_3 + 992 \ z_5 \tag{17}$$

where Soil pH (H_2O) and pH (KCl) are pH values for readings taken in 2:1 soil:water and soil:KCl suspensions, respectively; Soil Zn, P, and

Ca are extractable Zn, P, and Ca in ppm of air-dry soil, respectively; and z_1, z_3, z_4, and z_5 refer to coded treatment variables Zn (linear), P (linear), P (quadratic), and Ca (linear) in kg/ha, respectively.

As observed for the jaraguagrass pot study, lime was the major factor in affecting soil reaction and extractable nutrients. When the soil was limed, soil pH values were increased by 0.79 to 0.86 pH units, and as a result extractable Zn and P were decreased by approximately 40 and 20%, respectively. The adsorbent properties of lime may have also contributed to the reduction in extractable Zn and P values. Extractable Ca was increased by approximately 60% in limed soils. Direct and indirect effects of liming on various chemical and micro-biological processes must also have contributed to the responses obtained.

Although Zn applications demonstrated a significant effect in in-creasing extractable Zn, suppressive influence of higher pH values from liming nullified this effect. Zinc had no influence on extract-able P.

Phosphorus treatments significantly increased extractable P and, at the high P_2 rate, increased extractable Ca and soil pH (KCl) to a small but statistically significant level. The unusual properties of monocalcium phosphate in the soil may account for the significant extractable Ca and soil reaction responses.

Soil Nitrogen

Average values of total soil N for composite samples were 0.36 and 0.37% for control and fertilized (P_2, Zn_2, and Ca_1 treatment) soils, respectively. Mean total N values for control and fertilized (N_2, P_2, Zn_2, and Ca_1 treatment) soils from the jaraguagrass pot soils were 0.41 and 0.37%. It would appear that hairy indigo effectively lowered soil

N reserves to a relatively constant level since both control and fer-
tilized soil had similar total N concentrations. Appreciable leaching
of soil reserves seems unlikely in Santa Fe surface soils which are
high in interlayered 2:1 type clay minerals and organic matter.

Comparison Between Control and Fertilized Hairy Indigo

Appendix Table 84 shows the comparison of yields and elemental
composition between control and fertilized (P_2, Zn_2, and Ca_1 treatment)
hairy indigo. Full fertilizer treatment increased forage yields of
hairy indigo by between 37 to 70%, over control. Forage Zn concentra-
tions of fertilized hairy indigo were slightly lower than control due
to dilution effect of yield increase but total Zn uptake values were
increased by 50 to 70%. Both P and Ca compositions of fertilizer hairy
indigo were increased by two- to three-fold. It was interesting to
note that hairy indigo crown-root systems showed little response to
fertilizer amendments in contrast to the forage. Both jaraguagrass
forage and crown-root systems were responsive to applied nutrients.
This implies that rooting density was a major factor in the rate at
which the soil was depleted. A limited root system, similar to that
of hairy indigo, depletes the soil in the vicinity of roots more
effectively than a well-developed root system (similar to that of jara-
guagrass) which has a relatively large soil volume at its disposal.
This is especially true within the surface soil where resistance to
nutrient transfer is very small.

Effect of Hairy Indigo and Fertilizer on Pot Soils

Soil reaction and extractable nutrients of untreated (prior to
experiment), control, and fertilized (P_2, Zn_2, and Ca_1 treatment) soils

from the hairy indigo pot study are compared in Appendix Table 85.
Cropping without complete fertilizer treatment (control) decreased
soil pH from 5.40 to 5.10 pH (H_2O) and 4.33 to 4.10 pH (KCl), and de-
creased extractable Zn and Ca by 76 and 30%, respectively, from un-
treated soils. Compared with untreated soil, cropped and fertilized
soils increased pH by 0.50 (H_2O) and 0.63 (KCl) pH units, extractable
Ca by 13% and decreased extractable Zn by 80%. Increase in soil pH
by liming reduced extractable Zn although soil Zn reserves may have
been higher than untreated soil. Cropping seemed to have increased
extractable P values by 56% over untreated soil. The increase may have
been due to P mineralization from inorganic and organic P sources in
the soil. Fertilized and cropped soil gave a high extractable P value
of 32.8 ppm, which was 140% higher than untreated soil.

In comparison with corresponding soils values from the jaraguagrass
pot study, hairy indigo pot soils recorded lower soil pH (H_2O) values
by 0.2 - 0.4 pH units, and higher extractable P. The addition of urea
in fertilized jaraguagrass for soils could have been responsible for
these differences.

Nutrient Recovery

Nutrient recoveries of applied Zn, P, and Ca from the hairy indigo
pot study are given in Appendix Table 86. These values were calculated
in the same manner as described for jaraguagrass pot study and were
subject to similar errors. Again, these estimates are for comparative
evaluations. Recovery values were generally low as for jaraguagrass
pot study.

Lack of response to applied Zn by hairy indigo forage and crown-
root systems was evident in the relatively low Zn recoveries of 0.36

and 0.12% for Zn_1 rate and 0.19 and 0.02% for Zn_2 rate for the forage and crown-root system, respectively. In contrast to jaraguagrass, forage Zn recoveries by hairy indigo were three and nine times higher than crown-root systems for Zn_1 and Zn_2 rates, respectively. Despite the low Zn recoveries and limited root system, hairy indigo was more efficient than jaraguagrass in absorbing and accumulating Zn in the forage. Between 78 and 83% of the total Zn uptake by jaraguagrass, however, was recovered in the crown-root systems. Estimated extractable Zn for hairy indigo pot soils were 50 and 24% lower for Zn_1 and Zn_2 rates, respectively, than jaraguagrass pot soils.

Phosphorus recoveries by hairy indigo forage and crown-root systems were estimated to be 16.30 and 0.38% for P_1 rate and 9.78 and 0.39% for P_2 rate, respectively. Forage P recoveries were 40 and 25 times greater for P_1 and P_2 treatments, respectively, than crown-root systems of hairy indigo. Total P recovery by hairy indigo at the P_i rate was about 7% higher than at the P_2 rate. In contrast to jaraguagrass, hairy indigo forage P recoveries were 11.09 and 6.84% higher for the P_1 and P_2 rates, respectively. This clearly illustrates the relative efficiency of the legume rooting system.

It was surprising to observe that Ca recovery by hairy indigo crown-root systems was negligible, however, forage recovery of applied Ca was 2.31%. This was 1.49% higher than the recovery by jaraguagrass forage and 9.84% higher than by the entire jaraguagrass plant.

Field Experiments

Field experiments were established with the hope that four harvests might be obtained during a one-year period from each of the six experiments located at Santa Fe, Patino, and Yaviza in eastern Panama. All

experiments were sampled 21 days after the studies were initiated. However, it was only feasible to obtain second harvests at Santa Fe and Yaviza before the field experiments had to be abandoned. Insufficient time elapsed from establishment of the field studies to the second harvests to fully evaluate the effect of treatments on forage response, especially in the mixed sward trials. Forage and soil data from these experiments were, however, submitted for statistical analysis and have been documented for comparative purposes.

A summary of F tests from the analysis of variance on forage yields and elemental composition of jaraguagrass from all field experiments is presented in Appendix Table 87. Analysis of variance for the corresponding soil data only revealed statistical significance for two specific responses, hence the F test summary for soil values was not tabulated. These values will be mentioned in the text.

Jaraguagrass Field Experiments

Forage harvests and the corresponding soil samples were obtained 21 days after the establishment of the experiments at Patino, Yaviza, and Santa Fe. A second harvest was secured at Santa Fe 112 days after the first.

Yield

Oven-dry forage yields ranged from 104 kg/ha at Yaviza to 2,040 kg/ha for the second harvest at Santa Fe.

Yields of jaraguagrass forage harvested from the three experimental locations are shown in Table 60. In general, forage yields were inconsistent in response to fertilizer treatments for the first harvest, although the Zn_0 treatment at Santa Fe was significantly higher than other treatments. Yields were higher for fertilized plots than control

Table 60. Effect of Zn and fertilizer amendments on oven-dry yields of jaraguagrass forage from field experiments.

Treatment[1]	Patino	Yaviza	Santa Fe	
			Harvest	
	1	1	1	2
			kg/ha	
Control	367 a[2]	277 a	930 a	1,240 a
Zn_0	180 a	317 a	1,510 b	1,497 a
Zn_1	353 a	207 a	980 a	1,733 a
Zn_2	197 a	233 a	813 a	1,673 a

[1] Control plots were not fertilized and treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only), 100 kg N/ha, and 100 kg P/ha.

[2] Values followed by the same letter in each column are not significantly different at 0.05 probability level.

at Santa Fe (second harvest) but were not statistically different. Jaraguagrass swards at Patino and Yaviza were less dense and physiologically older compared to the sward at Santa Fe. Partly for these reasons and the fact that lime was also applied in the fertilizer treatments, forage yields at Santa Fe were three- to four-fold higher than recorded at Patino or Yaviza. Forage yields at Santa Fe ranged from 935 to 2,036 kg/ha for the second harvests. These values were comparable to measurements from the jaraguagrass pot experiment which averaged the equivalent of 1,320, 1,400, and 1,970 kg/ha for the three forage harvests. Tergas (243) reported dry season yields of jaraguagrass in Costa Rica to be between 3,143 and 4,971 kg/ha for grass cut 115 days after N fertilization. Lower forage yields recorded at Santa Fe during the rainy season were probably due to the grass being physiologically younger and having lower crude fiber contents.

Effects of Zn and fertilizer amendments on Zn, P, and Ca compositions of jaraguagrass forage are presented in Table 61.

Zinc concentration and total uptake

Forage Zn concentration values ranged from 20 ppm Zn at Yaviza to 285 ppm Zn for the first harvest at Santa Fe. Control forage Zn concentrations were between 21 to 29 ppm Zn for all three locations. Only Yaviza and Santa Fe (first harvest) demonstrated significant ($P = 0.01$ and $P = 0.05$, respectively) responses to Zn and fertilizer applications although high Zn concentration values were recorded for forage harvested from Patino. The unusually high forage Zn concentrations of 52 to 184 ppm for the first harvest Zn_2 treatment at the three locations may be attributed to foliar absorption of applied Zn since the treatment was sprayed on the stubble and young growth of each plot. By the second

Table 61. Effect of Zn and fertilizer amendments on Zn, P, and Ca compositions of Jaraguagrass forage from field experiments.

	Concentration				Total uptake			
	Patino	Yaviza	Santa Fe		Patino	Yaviza	Santa Fe	
	Harvest				Harvest			
Treatment[1]	1	1	1	2	1	1	1	2
	ppm				kg/ha			
				Zn				
Control	29 a[2]	21 a	26 a	28 a	0.011 a	0.006 a	0.024 a	0.035 a
Zn0	28 a	26 ab	27 a	32 a	0.005 a	0.009 a	0.040 ab	0.047 a
Zn1	73 a	52 b	52 a	27 a	0.026 b	0.010 a	0.059 ab	0.046 a
Zn2	70 a	126 c	184 b	38 a	0.014 ab	0.029 b	0.161 b	0.055 a
				P				
Control	2,160 a	3,700 a	2,590 ab	2,700 a	0.78 a	1.01 a	2.43 a	3.18 a
Zn0	2,940 b	3,240 a	2,280 a	2,930 a	0.53 a	1.03 a	3.46 a	4.40 a
Zn1	3,110 b	2,750 a	2,480 ab	3,010 a	1.12 a	0.56 a	2.43 a	5.21 a
Zn2	3,340 b	3,630 a	3,000 b	3,110 a	0.64 a	0.84 a	2.42 a	5.25 a

Table 61. Continued

Treatment[1]	Concentration				Total uptake			
	Patino	Yeviza	Santa Fe		Patino	Yeviza	Santa Fe	
	Harvest				Harvest			
	1	1	1	2	1	1	1	2
	------- ppm -------				------- kg/ha -------			
				Ca				
Control	4,460 a	5,010 a	3,720 a	3,410 a	1.63 a	1.37 a	3.55 a	4.13 a
Zn0	4,480 a	4,630 a	3,970 ab	3,850 a	0.80 a	1.46 a	5.97 b	5.89 a
Zn1	4,430 a	4,230 a	4,580 b	3,790 a	1.60 a	0.84 ab	4.53 ab	6.53 a
Zn2	4,390 a	4,860 a	4,320 ab	4,158 a	0.86 a	1.11 a	3.41 a	7.03 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only), 100 kg N/ha, and 100 kg P/ha.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

harvest at Santa Fe the forage Zn concentration levels were between
normal limits of 21 to 48 ppm and no significant treatment differences
were found.

Total Zn uptake values were significantly higher than control for
the Zn_1 rate at Patino and Zn_2 rate at Yaviza and Santa Fe (first
harvest). Inconsistent yield data, however, make total nutrient up-
take values difficult to interpret.

In general, Zn compositional values of jaraguagrass forage from
the Santa Fe study were essentially similar to those recorded for the
jaraguagrass pot trial. Average total forage Zn uptake at Santa Fe
(second harvest) was 0.064 kg Zn/ha compared to an average of 0.052
kg Zn/ha for jaraguagrass (second harvest) pot study.

Phosphorus concentration and total uptake

Phosphorus concentration values of jaraguagrass forage ranged from
1,940 ppm P at Santa Fe for the second harvest to 4,960 ppm P at Yaviza.

A significant (P = 0.05) P concentration response was observed at
Patino for fertilized jaraguagrass forage over control. Fertilized
forage P concentration values were over 40% higher than the mean value
of 2,160 ppm P recorded for control. The Zn_2 treatment at Santa Fe
(first harvest) resulted in higher forage P concentration than found
for Zn_0 and control treatments. No consistent significant differences
in forage P concentrations were observed for the Yaviza and Santa Fe
(second harvest) trials. Availability of indigenous P in Yaviza soils
and the application of lime at Santa Fe probably accounted for the
lack of significant responses. Generally, forage P concentration values
from Santa Fe plots were about 50% lower than recorded for the jaragua-
grass pot study.

Total forage P uptake values were not significant due to the high variability in forage yields. A reflection of higher yields was evident in the greater total P uptake values obtained for Santa Fe harvested forage compared to Yaviza and Patino. In general, the equivalent total forage P uptake values for jaraguagrass pot study were about 1.3 kg P/ha lower than values recorded for the Santa Fe field trial.

Calcium concentration and total uptake

Concentration values for jaraguagrass forage Ca ranged from 3,000 ppm at Santa Fe for the first harvest to 5,688 ppm Ca at Yaviza. Limed plots at Santa Fe (first harvest) gave higher forage Ca concentration values than control but only the Zn_1 treatment was significantly different. No significant response to lime was observed at Santa Fe by the second harvest although actual forage Ca concentration values were between 380 and 750 ppm Ca higher than control. Since lime was not applied for the Patino and Yaviza experiments, no significant differences in forage Ca concentrations were expected or found.

Total Ca uptake by jaraguagrass forage was only found to be significant for the Zn_0 treatment at Santa Fe (first harvest) which was a reflection of the significantly high forage yield recorded.

Forage Ca compositions from jaraguagrass pot experiments were generally 20-25% higher than for values recorded in the Santa Fe field study.

Nitrogen and crude protein

Jaraguagrass forage from the control and Zn_2 (with fertilizer) plots from each field experiment was analyzed for N. Average forage N concentrations for control and Zn_2 plots at Santa Fe were 1.10 and

1.30%, respectively, for the first harvest which were equivalent to 6.90 and 8.10% crude protein (CP), respectively. Nitrogen concentrations in the second Santa Fe harvests were 1.00% N (6.25% CP) for both control and Zn_2 plots, respectively. First forage harvest N values were 1.00 and 1.40% N (6.25 and 8.80% CP) at Yaviza and 2.00 and 2.92% N (12.50 and 18.25%) at Patino, for control and Zn_2 plots, respectively. Unusually high N and CP values obtained for forages from Patino were indicative of the immature stage of the jaraguagrass regrowth at the time of sampling. Forage N concentrations recorded at Santa Fe and Yaviza were similar to those reported for the jaraguagrass pot study. Complete fertilizer and Zn_2 resulted in higher N% in the first forage harvest at all locations but the effect of applied N appeared to have diminished for the second harvest at Santa Fe. Since the interval between harvests at Santa Fe was 112 days, the forage N values averaging 1.00% were within normality.

Other elemental concentrations

Data in Appendix Table 88 show the concentrations of Mg, Fe, Cu, Mn, and Sr in jaraguagrass forage harvested from Patino, Yaviza and Santa Fe. With the exception of Mn differences at Patino and Mn and Fe responses at Yaviza, no aberrant elemental values were significant as a result of applied treatments. Magnesium concentrations of forage were between 280 and 930 ppm higher at Santa Fe than found at Patino or Yaviza. The effect of lime was also evident at Santa Fe in reducing forage Fe concentrations over control but the differences were not significant. Copper values in the forage were notably lower in the second Santa Fe harvest compared to the first. Santa Fe forage elemental values were essentially similar to those found for the jaraguagrass

pot experiment although Mg levels seem to be generally higher for field experiment forages, probably due to the presence of Mg in the commercial lime source used.

Soil pH and extractable nutrients

Soil pH (H_2O) values ranged from pH 5.0 at Santa Fe for the second harvest to pH 7.1 at Yaviza. Extractable Zn varied from 0.2 (Santa Fe, second harvest) to 4.9 ppm Zn (Santa Fe, first harvest). Extractable P and Ca ranged from 0.4 ppm P (Santa Fe, first harvest) to 40 ppm P (Santa Fe, second harvest) and 1,670 ppm Ca (Patino) to 7,340 ppm Ca (Yaviza), respectively.

Soil pH.--Despite addition of lime in the Santa Fe jaraguagrass field study, no statistically significant differences were observed for soil pH (H_2O) between fertilized plots and control (Table 62). However, fertilized plots at Santa Fe (first harvest) did show that average soil pH (H_2O) values were 6.25 compared to control value of pH 5.63. By the second harvest period the effect of lime on pH was not evident at Santa Fe. This was indicative of the high buffering capacity of the soil which was also demonstrated by the jaraguagrass pot study soils. Both Patino and Yaviza soils were neutral in soil reaction and averaged pH (H_2O) 6.55 and 6.80, respectively.

Effects of Zn and fertilizer amendments on extractable Zn, P, and Ca from jaraguagrass field experiment soils are summarized in Table 63.

Extractable Zn.--The Zn_2 treatment at Santa Fe (second harvest), was significantly ($P = 0.01$) higher than other treatments in extractable Zn. Although no significant values were found, Zn_1 and Zn_2 treatments at Yaviza and Santa Fe (first harvest) showed higher extractable Zn values than Zn_0 and control. No differences were found for Patino soils. In general, extractable Zn values were low for soils in all

Table 62. Effect of Zn and fertilizer amendments on pH (H_2O) of soils from jaraguagrass field experiments.

Treatment[1]	Patino	Yaviza	Santa Fe	
			Harvest	
	1	1	1	2
Control	6.67 a[2]	6.83 a	5.63 a	5.50 a
Zn_0	6.37 a	6.80 a	6.30 a	5.47 a
Zn_1	6.60 a	6.70 a	6.17 a	5.73 a
Zn_2	6.57 a	6.87 a	6.30 a	6.10 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1 and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only), 100 kg N/ha, and 100 kg P/ha.

[2]Values followed by the same letter in each column are not significantly different at 0.05 probability level.

Table 63. Effect of Zn and fertilizer amendments on extractable Zn, P, and Ca of soils from jaraguagrass field experiments.

Treatment[1]	Patino	Yaviza	Santa Fe	
			Harvest	
	1	1	1	2
	ppm			

Zn

Treatment[1]	Patino	Yaviza	Santa Fe	
Control	1.3 a[2]	1.2 a	1.7 a	0.4 a
Zn_0	1.4 a	1.2 a	1.9 a	0.3 a
Zn_1	1.3 a	1.7 a	2.8 a	0.5 a
Zn_2	1.4 a	2.1 a	2.5 a	1.3 b

P

Control	2.8 b[2]	6.5 a	9.8 a	17.4 a
Zn_0	5.6 a	13.1 b	6.4 a	11.3 a
Zn_1	3.3 a	20.1 c	12.0 a	21.4 a
Zn_2	2.3 a	16.8 bc	6.8 a	26.9 a

Ca

Control	3,070 a[2]	6,470 a	3,700 a	3,430 a
Zn_0	3,490 a	6,480 a	6,470 a	2,840 a
Zn_1	3,560 a	6,630 a	5,300 a	3,720 a
Zn_2	3,550 a	6,730 a	5,170 a	4,340 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1 and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only) 100 kg N/ha, and 100 kg P/ha.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

locations. The effect of liming in reducing extractable Zn was not evident at Santa Fe but declined to very low levels by the second harvest period. These values were only slightly lower than for the pot soils.

Extractable P.--Only the Yaviza experimental soils showed significant ($P = 0.01$) increases in extractable P over control. Extractable P value in the control plot was 6.5 ppm P compared to 13.1, 20.1, and 16.8 ppm P for fertilized Zn_0, Zn_1, and Zn_2 plots, respectively. Extractable P values were statistically the same for Patino and Santa Fe treated soils and control. Santa Fe and Yaviza soils, which received P fertilizer, showed moderate to high values but extractable P values of between 2.3 and 5.6 ppm recorded for Patino soils were considered low. Extractable P values for jaraguagrass pot soils were similar to Santa Fe field study soils sampled at the second harvest period.

Extractable Ca.--No significant effect between fertilized and control treatments was observed. This was surprising for Santa Fe soils since lime had been applied. However, extractable Ca values for limed plots of Santa Fe (first harvest) were higher than control by between 40 and 75%. The high degree of sample variabilities no doubt accounted for the insignificant values. Extractable Ca values of over 6,400 ppm Ca found for Yaviza soils were considered high. Santa Fe (second harvest) and Patino soils recorded relatively lower extractable Ca values of between 2,840 and 4,340 ppm Ca.

Soil nitrogen

Average total soil N values for control and Zn_2 plus fertilizer treatments were not significantly different for all samples collected during the first harvest. The mean total soil N contents were 0.28,

0.21, and 0.33% for Patino, Yaviza, and Santa Fe experiments, respec-
tively. By the second harvest at Santa Fe, average soil N was 0.35
and 0.28% for control and Zn_2 plots, respectively. Presumably the
addition of fertilizers and subsequent increase in plant growth had
drained the soil N reserves at Santa Fe. Control and fertilizer-treated
soils for jaraguagrass pot study averaged 0.41 and 0.37% total N,
respectively.

Mixed Sward Field Experiments

The mixed sward (jaraguagrass-hairy indigo) field experiments were
established to compare the response of the grass and legume grown and
treated under the same conditions. Once fully established the legume
was expected to supply N through its symbiotic association with rhizobia
in root nodules. Consequently, N fertilizer was omitted from fertil-
izer treatments which were otherwise the same as for jaraguagrass field
experiments. Hairy indigo, however, was relatively slow to establish
and demonstrate its complementary effect on the sward. Only jaragua-
grass forage samples were obtained from the first harvests at each
location which were made 21 days after establishment. Santa Fe mixed
sward was harvested a second time 112 days after the first harvest and
again only jaraguagrass samples were obtained as the legume had not
grown sufficiently for cutting. A second harvest was also obtained
from Yaviza[1] (63 days after the first harvest) at which time both jara-
guagrass and hairy indigo forages were sampled. However, forage yield

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[1] Collected by Drs. J. F. Gamble, S. C. Snedaker, and N. H.
Nickerson, University of Florida Agricultural Ecology Team.

assessments could not be made at Yaviza because the experimental area had been grazed by stray cattle.

Forage and soil data collected from the mixed sward field experiments have been included and tabulated for general reference and comparative purposes. These experiments were conducted adjacent to the jaraguagrass field experiment at each location and the only treatment difference between the two studies was the absence of applied N in the fertilizer treatments of the mixed sward plots. Analytical results in response to treatments were essentially similar to the jaraguagrass field trial and, except for minor aberrations, the discussion would merely be repetitious.

Effect of Zn and fertilizer amendments on yields and elemental composition of jaraguagrass forage from the mixed sward field experiments is presented in Tables 64 and 65, respectively. The corresponding data on soil reaction and extractable nutrients are given in Tables 66 and 67, respectively. Treatment effects on Mg, Fe, Cu, and Mn concentrations of jaraguagrass forage from the mixed sward field experiment are shown in Appendix Table 89. Elemental concentrations of hairy indigo forage harvested from Yaviza mixed sward field experiment are given in Appendix Table 90 with respect to the Zn and fertilizer treatments.

The difficulty of obtaining precise measurements in field experiments, because of inability to control numerous environmental variables, is generally known and appreciated. Despite this and various economic considerations, field experiments do reflect and actual soil-plant relationship as it exists under natural conditions (75). While pot experiments indicate the amount of available nutrient per unit volume of

Table 64. Effect of Zn and fertilizer amendments on oven-dry yields
of jaraguagrass forage from the mixed sward field experiments.

Treatments[1]	Patino	Yaviza	Santa Fe	
			Harvest	
	1	1	1	2
	---------------------- kg/ha ----------------------			
Control	413 b[2]	290 a	533 a	1,440 a
Zn_0	340 b	310 a	350 a	1,233 a
Zn_1	330 b	220 a	660 a	1,347 a
Zn_2	143 a	247 a	390 a	1,083 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1, and Zn_2
were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with
an equivalent application of 2,000 kg Ca/ha (Santa Fe only), and 100 kg
P/ha.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

Table 65. Effect of Zn and fertilizer amendments on Zn, P, and Ca compositions of jaraguagrass forage from the mixed sward field experiments.

Concentration (ppm)

Treatment[1]	Patino Harvest 1	Yaviza Harvest 1	Yaviza Harvest 2	Santa Fe Harvest 1	Santa Fe Harvest 2
Zn					
Control	22 a[2]	19 a	29 a	23 a	25 a
Zn0	23 a	20 a	35 a	32 a	26 a
Zn1	145 a	55 b	53 b	41 a	29 a
Zn2	180 a	40 b	69 c	61 b	25 a
P					
Control	1,600 a[2]	3,360 a	2,280 a	3,280 a	2,910 a
Zn0	3,280 b	3,960 b	2,680 ab	3,290 a	2,990 a
Zn1	3,640 c	3,930 b	2,890 b	3,180 a	3,060 a
Zn2	3,170 b	3,770 b	2,540 ab	3,410 a	3,280 a

Total uptake (kg/ha)

Treatment[1]	Patino Harvest 1	Yaviza Harvest 1	Santa Fe Harvest 1	Santa Fe Harvest 2
Zn				
Control	0.009 a	0.005 a	0.013 a	0.038 a
Zn0	0.008 a	0.006 a	0.015 a	0.033 a
Zn1	0.056 a	0.013 a	0.027 a	0.041 a
Zn2	0.023 a	0.010 a	0.070 b	0.027 a
P				
Control	0.65 ab	0.95 a	1.80 a	4.15 a
Zn0	1.11 b	1.23 a	1.06 a	3.69 a
Zn1	1.16 b	0.86 a	2.12 a	4.07 a
Zn2	0.46 a	0.94 a	1.31 a	3.56 a

Table 65. Continued

	Concentration (ppm)					Total uptake (kg/ha)			
	Patino	Yaviza		Santa Fe		Patino	Yaviza	Santa Fe	
	Harvest					Harvest			
Treatment[1]	1	1	2	1	2	1	1	1	2
			Ca						
Control	4,880 a[2]	4,750 a	3,790 a	3,610 a	3,750 a	2.00 b	1.32 a	1.96 a	5.28 a
Zn_0	5,230 a	4,910 a	3,740 a	4,200 a	3,970 a	1.85 b	1.52 a	1.48 a	4.89 a
Zn_1	5,020 a	4,770 a	4,090 a	3,970 a	3,930 a	1.65 b	1.07 a	2.71 a	5.17 a
Zn_2	4,540 a	4,670 a	3,770 a	3,770 a	3,920 a	0.65 a	1.17 a	1.52 a	4.28 a

[1] Control plots were not fertilized and treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only), and 100 kg P/ha.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

Table 66. Effect of Zn and fertilizer amendments on pH (H_2O) of soils
from the mixed sward field experiments.

Treatment[1]	Patino	Yaviza		Santa Fe	
		Harvest			
	1	1	2	1	2
Control	7.00 b[2]	6.87 a	6.67 a	5.40 a	4.87 a
Zn_0	6.73 ab	6.77 a	6.73 ab	5.70 a	6.03 ab
Zn_1	6.70 ab	6.90 a	6.77 b	5.73 a	5.07 ab
Zn_2	6.57 a	6.93 a	6.73 ab	5.73 a	6.10 b

[1]Control plots were not fertilized and treatments Zn_0, Zn_1, and Zn_2
were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with
an equivalent application of 2,000 kg Ca/ha (Santa Fe only), and 100 kg
P/ha.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

Table 67. Effect of Zn and fertilizer amendments on extractable Zn, P, and Ca of soils from the mixed sward field experiments.

Treatment [1]	Patino	Yaviza		Santa Fe	
		Harvest			
	1	1	2	1	2
			ppm		
			Zn		
Control	1.0 a[2]	1.6 a	0.8 a	2.3 a	0.5 a
Zn_0	1.2 a	1.1 a	1.1 a	3.2 a	0.6 a
Zn_1	3.1 a	1.8 a	5.3 a	2.7 a	0.7 a
Zn_2	1.3 a	2.6 a	1.8 a	2.0 a	0.9 a
			P		
Control	7.6 a[2]	7.5 a	10.3 a	5.8 a	11.8 a
Zn_0	3.0 ab	8.4 a	9.1 a	8.6 a	23.8 a
Zn_1	4.9 b	9.8 a	11.2 a	28.0 a	16.1 a
Zn_2	4.4 b	7.0 a	12.1 a	9.1 a	24.4 a
			Ca		
Control	3,520 a[2]	6,430 a	6,970 a	3,240 a	2,280 a
Zn_0	3,360 a	6,230 a	7,600 a	3,680 a	4,440 a
Zn_1	3,620 a	6,480 a	7,770 a	4,120 a	2,930 a
Zn_2	3,260 a	6,260 a	7,100 a	3,900 a	4,200 a

[1] Control plots were not fertilized and treatments Zn_0, Zn_1 and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only), and 100 kg P/ha.

[2] Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

soil, field studies reflect the actual volume of soil from which a plant obtains its nutrients. Since the field experiments conducted in eastern Panama were relatively short in duration, yield responses were not consistent and thus total nutrient uptake values were difficult to assess relative to treatment effects. Since it was only feasible to replicate treatments three times only 6 degrees of freedom were available for estimation of error. Despite obvious trends to fertilizer treatments, the high degree of variability resulted in many insignificant responses. However, values obtained from these experiments indicated forage nutrient concentration ranges in response to treatments and gave quantitative information of total nutrient uptake. In general, data from the jaraguagrass pot experiment were in close agreement with those from the Santa Fe jaraguagrass field study.

In summary, data from the field experiments generally indicated the high inherent fertility of the three soils selected for this study. Each soil was specific in responding to fertilizer treatments, as reflected in the plant tissue or soil analyses. Most of the responses were not statistically different but trends were obvious.

Santa Fe soils were strongly acid and demonstrated positive trends to lime application in the first harvest with relatively higher pH values, extractable Ca, and jaraguagrass forage Ca concentrations over control. Application of Zn gave higher extractable and forage Zn concentrations over Zn and control treatments. By the second harvest period the soil pH had declined in the limed. Extractable Zn and Zn composition of forage were similar to control, while extractable P and Ca and forage P and Ca concentrations had increased.

Yaviza soils were neutral in reaction and demonstrated positive

response to Zn applications with relatively higher extractable Zn and jaraguagrass and hairy indigo forage Zn values relative to control. Extractable Zn and P values were low, probably due to the high inherent soil pH.

Patino soils were also neutral in soil reaction and showed definite increases in forage Zn and P concentrations in fertilized plots although extractable nutrient values were relatively low.

These major soils studied were inherently fertile, capable of retaining applied nutrients against leaching (85) while maintaining a relatively large supply of the nutrients for crop absorption.

SUMMARY AND CONCLUSIONS

Two pot and six field experiments were established in the Darien Province of eastern Panama during the rainy season to study the effect of applied nutrients on zinc uptake by jaraguagrass (<u>Hyparrhenia rufa</u> (Nees) Stapf) and hairy indigo (<u>Indigofera hirsuta</u> L.) in selected eastern Panamanian soils.

Soils selected for study at Santa Fe, Patino and Yaviza field experimental locations were characterized and sampled for laboratory analyses. Surface soil (0 - 15 cm) collected from Santa Fe was used for the pot experiments.

The two pot experiments were conducted, under semi-controlled conditions, at Santa Fe to determine the effect of various levels of nitrogen (N), phosphorus (P), calcium (Ca), and zinc (Zn) on Zn uptake by jaraguagrass and of P, Ca, and Zn on Zn uptake by hairy indigo. Factorially arranged, completely randomized block designs were used for both the jaraguagrass and hairy indigo pot studies. Replicated three times, treatments for the jaraguagrass pot experiment were as follows: (a) three levels of N (0, 50, and 100 kg N/ha/harvest applied as urea); (b) three levels of P (0, 50, and 100 kg Ca/ha applied as monocalcium phosphate; (c) two levels of Ca (0 and 2,000 kg Ca/ha applied as lime); and (d) three levels of Zn (0, 15, and 30 kg Zn/ha applied as zinc sulfate). In addition, each pot received a basic dressing equivalent to 90 kg K/ha as potassium sulfate. Jaraguagrass forage was harvested three times; 54, 96, and 126 days after germination.

Immediately following the final forage harvest, crown-root systems and soil samples were collected for analyses.

Oven-dry yields of jaraguagrass forage ranged from 0.59 to 8.20 g/pot (equivalent to 320 and 4,460 kg/ha) and crown-root yields from 4.02 to 20.16 g/pot (equivalent to 2,190 and 10,970 kg/ha). Average yields were 2.43, 2.58, 3.62, and 8.63 g/pot (1,320, 1,400, 1,970 and 4,690 kg/ha) for the three forage harvests and crown-root harvest, respectively.

Calcium in the form of lime had the most profound effect on jaraguagrass responses and soil conditions. Liming significantly increased both forage and crown-root yields by 33 to 85%. Soil pH was increased significantly by liming from pH (H_2O) 5.43 to 6.17 and pH (KCl) 4.15 to 4.99. Primary effect of lime may be attributed to the increase in soil pH which in turn may have stimulated plant growth by influencing various soil fertility factors. As an essential nutrient, Ca also plays an important role in plant yield increases. Applied N significantly increased forage and crown-root yields by 33 to 80%. After the first harvest forage yields from N_1 and N_2 treatments were essentially the same. Lime x N interactions were significant and generally enhanced jaragaugrass yields after the first harvest.

Although Zn levels had no significant effect on forage yields, a positive incipient trend was observed in the first harvest. Negative N x Zn interactions were found for the second forage harvest and crown-root yields. Zinc, at the Zn_2 level, significantly increased crown-root yields by 8% over Zn_0 treatment. Except for the first harvest when P_1 and P_2 rates increased forage yields over P_0 treatment, no consistent effect of applied P on forage or crown-root yields was found

significant. Second-order interactions of N x P x Ca, N x Ca x Zn, and N x P x Zn were significant for the first, second and third harvests, respectively.

Jaraguagrass Zn concentrations ranged from 12 to 89 ppm for the forage and 51 to 880 ppm for the crown-root systems. Zn concentrations averaged 22, 40, 43, and 157 ppm for the three forage harvests and crown-root harvest, respectively. Mean total Zn uptake for the three forage harvests and crown-root harvest was 55, 101, 137, and 1,449 ug/pot (equivalent to 0.03, 0.06, 0.08, and 0.79 kg Zn/ha), respectively. Soil-extractable Zn ranged from 0.1 to 3.6 ppm.

Applied Zn significantly increased extractable Zn by 37 to 57% over Zn_0 but the mean values of 0.80 and 0.91 ppm Zn were considered low. This was partly attributed to the use of $1\underline{N}$ NH_4OAc (pH 7) extractant when actual soil pH values in the soil were considerably lower. Zinc concentrations of jaraguagrass forage and crown-root systems were significantly increased by Zn increments. Except for the first forage harvest, Zn concentration values in jaraguagrass forage were considered relatively high (35 - 50 ppm) which belied the low soil Zn extraction data. The assumptions are that soil Zn was actually more available under the experimental conditions and that jaraguagrass was relatively efficient in absorbing soil Zn. The effect of Zn on total forage Zn uptake was largely mollified by its minor effect of forage yields. However, Zn_2 treatment did significantly increase total forage Zn uptake over Zn_0 by 22%. In addition to stimulating yields, Zn significantly increased total Zn uptake of crown-root systems over control by 36 - 87%.

Extractable Zn was found to be inversely related to soil pH and liming. Addition of lime and the concomitant increase in soil pH

probably resulted in a decrease of the plant-available form of Zn^{++},
decrease in solubility of pH-dependent forms of Zn, increase in Zn
absorption or precipitation, change in stability of soluble and in-
soluble organic complexes, and other indirect effects. Liming de-
creased jaraguagrass forage and crown-root Zn concentrations. In-
creased plant yields, as a result of liming, may have lowered Zn con-
centration values by the dilution effect but significantly increased
total Zn uptake values of the forage and crown-root systems.

The interaction of applied N and P significantly affected extract-
able Zn and implied that at high application rates of these fertilizers,
availability of Zn was generally depressed in the soil, presumably by
complex ion formation. Nitrogen, however, significantly increased for-
age Zn concentrations and forage and crown-root Zn uptake mainly through
its stimulating effect on plant growth in general. Except for the first
forage harvest, a synergistic effect of N x Zn interactions on increas-
ing forage and crown-root Zn concentrations was observed. The negative
effect of lime was buffered by N in the N x Ca interactions on Zn forage
concentrations of the first and second harvests. However, positive N
x Ca interactions were operative on total forage Zn uptake for the last
two harvests. Phosphorus had no consistent effect on extractable Zn
nor did it significantly affect Zn composition of jaraguagrass forage.
However, Zn uptake by the crown-roots was significantly increased by
applied P which suggested that Zn may be immobilized in the crown-root
systems or in the immediate vicinity of the roots. Estimated recoveries
of applied Zn by jaraguagrass forage and crown-root systems of 0.65 and
2.04% for Zn_1 treatment and 0.43 and 2.12% for Zn_2 rate, respectively,
were considered low. Forage Zn recoveries were 68 and 80% lower than

crown-root systems, for Zn_1 and Zn_2 levels, respectively. Over 97% of applied Zn was in the soil compartment of which only 1.5 - 2.0% was extractable. Since loss by leaching seemed unlikely in Santa Fe soils, Zn was probably adsorbed, precipitated, or fixed by inorganic and organic soil constituents.

Phosphorus concentrations of jaraguagrass forage ranged from 400 to 3,500 ppm and varied from 87 to 2,000 ppm in crown-root systems. Average forage P concentrations were 986, 1,473, and 1,285 ppm for the three harvests, respectively, while crown-root P concentrations averaged 533 ppm. Total P uptake values for jaraguagrass averaged 2.37, 3.61, 3.62, and 4.89 mg/pot (equivalent to 1.29, 1.96, 1.97, and 2.66 kg P/ha) for the three forage harvests and crown-root systems, respectively. Extractable P varied from trace to 59.5 ppm.

Phosphorus treatments significantly increased extractable P and jaraguagrass P concentration and total uptake values. The P composition of jaraguagrass forage and crown-root systems was significantly increased by liming despite the depressive effect of lime and the concomitant increase in soil pH on extractable P. Values for P composition of jaraguagrass were lower than expected in light of relatively high P extraction data but were adequate for normal plant growth. An incipient N x P interaction was observed on extractable P but its effect was minor in comparison to the positive effect of P applications. Nitrogen significantly decreased forage P concentrations (dilution effect of yield increase) but had an enhancement effect on increasing total P uptake only by the third forage harvest and crown-root systems. No effect of Zn treatments was observed for extractable P but a positive effect on total forage P uptake was recognized for the third harvest.

The relationship of applied nutrients with extractable P and jaragua-grass P composition was intricate and complex. Recoveries of applied P by jaraguagrass forage and crown-root systems were estimated to be 5.21 and 2.61% for the P_1 rate and 5.40 and 2.78% for the P_2 rate, respectively. About 92 to 95% of the applied P remained in the soil compartment of which approximately 24% was extractable P.

Jaraguagrass Ca concentrations varied from 2,750 to 11,000 ppm in the forage and 986 to 4,900 ppm in crown-root systems. Mean Ca con-centration in the three forage harvests and crown-root systems were 4,950, 5,390, 5,410, and 3,300 ppm, respectively. Total Ca uptake averaged 11.80, 13.62, 16.30, and 31.90 mg/pot (equivalent to 6.42, 7.41, 8.87, and 17.35 kg Ca/ha) for the three forage harvests and crown-root systems, respectively. Extractable Ca varied from 2,850 to 5,780 ppm.

As expected, lime increased Ca concentration and total uptake of jaraguagrass and soil-extractable Ca. Nitrogen significantly depressed forage Ca concentration (dilution effect) but increased total Ca uptake in the forage and crown-root systems through its effect on increased yields. The N_1 and N_2 treatments were similar in their effect of Ca nutrition of jaraguagrass. An N x P interaction had a positive but incipient effect on enhancing extractable Ca. While P had no effect on Ca concentration of jaraguagrass, it significantly increased total Ca uptake by the third forage harvest due to its effect on forage yields. Neither N nor P affected Ca concentration of roots. Zinc had a positive effect on total Ca uptake for the third forage harvest only. In common with P, the effect of applied nutrients on Ca composition of jaragua-grass was complex, especially by the third forage harvest. Estimated

recoveries by forage and crown-root systems of applied Ca were 0.82 and 0.65%, respectively.

Nitrogen concentrations of composite jaraguagrass forage samples ranged from 0.10 to 1.74% which corresponded to 0.625 to 10.88% crude protein. Application of N increased forage N concentrations in the first harvest from a mean of 0.95, 1.31, to 1.62% N and in the third harvest from 0.27, 1.36 to 1.37% N for N_0, N_1, and N_2 treatments, respectively. Results from the second harvest were inconsistent. Effect of cropping without N fertilizer was clearly demonstrated by the steady decline in forage N concentrations in control plots from 0.95 and 0.75 to 0.27 for the three harvests, respectively. Total N content of soil composite samples averaged 0.41, 0.40, and 0.39% for N_0, N_1, and N_2 treated soils, respectively. Nitrogen recoveries ranged from 15 to 56% for the first and second forage harvests. Recoveries from the N_2 rate were generally lower than N_1 rate, especially by the third harvest. Zinc levels had no overt effect on N concentration of forage.

Average concentrations of the other elements in jaraguagrass forage were 1,950 ppm Mg, 80 ppm Fe, 14 ppm Cu, 38 ppm Mn, and 37 ppm Sr.

Comparisons between control and fertilized (N_2, P_2, Zn_2, and Ca_1) jaraguagrass illustrated the tremendous capacity of the forage and, especially, crown-root systems to absorb and accumulate Zn and other applied nutrients. Zinc concentrations of fertilized jaraguagrass were 120 - 160% higher while total Zn uptake values were 260 to 300% higher than control.

Analytical values from untreated (prior to experiment), control, and fertilized (N_2, P_2, Zn_2, and Ca_1) jaraguagrass pot soils indicated

that, even over a short period of time, intensive cropping without addition of fertilizer would deplete soil nutrient reserves noticeably.

With the exception of N fertilizer, treatments and replication for the hairy indigo pot experiment were the same as for the jaraguagrass pot study. Forage harvests were made 66, 109, and 139 days after germination. Crown-root systems and soil samples were collected immediately following the last harvest.

Oven-dry yields of hairy indigo ranged from 0.87 to 6.21 g/pot (equivalent to 470 and 3,380 kg/ha) for forage and 1.12 to 2.86 g/pot (equivalent to 610 and 1,560 kg/ha) for crown-root systems. Average yields of hairy indigo for the three forage harvests and crown-root systems were 2.90, 4.03, 2.49, and 1.70 g/pot (equivalent to 1,580, 2,190, 1,360, and 925 kg/ha), respectively.

The dominant role of Ca, applied as lime, in soil reactions and hairy indigo responses was evident in this study. Lime significantly increased forage yields over control by 13 - 31%; however, crown-root systems show no significant yield response.

Calcium, as an essential element, was especially important in the mineral nutrition of hairy indigo. Neither Zn nor P had any significant effect on increasing yields of the legume. Although the Zn treatment showed a depressing effect on yields in general, total forage yields of hairy indigo exceeded corresponding yields of jaraguagrass by 9%. However, average crown-root yields of hairy indigo were only 18% of the yields recorded for jaraguagrass.

Zinc concentration values of hairy indigo ranged from 21 to 56 ppm for forage and 48 to 225 ppm for crown-root systems. Average Zn concentrations were 36, 41, 43, and 100 ppm for the three forage harvests

and crown-root harvest, respectively. Total Zn uptake by hairy indigo for the three forage harvests and crown-root systems averaged 106, 163, 104, and 173 ug Zn/pot (equivalent to 0.06, 0.09, 0.06, and 0.09 kg Zn/ha), respectively. Extractable Zn varied from 0.2 to 3.5 ppm.

An inverse relationship between extractable Zn and soil pH occurred in the hairy indigo pot study. However, in the absence of lime, extractable Zn and Zn concentration of hairy indigo forage and crown-root systems were significantly increased. The converse was true upon addition of lime. As previously mentioned, the decrease in extractable Zn with liming may be due to a number of pH-dependent chemical and bio-chemical processes operating in the soil. Despite low Zn extraction values and the negative relationship with lime, Zn concentration and total Zn uptake values of hairy indigo forage were relatively high in comparison with various forage legumes sampled in Panama and jaragua-grass from the pot study.

Except for the second forage harvest and crown-root systems, Zn applications did not significantly increase total Zn uptake by hairy indigo. Lime significantly increased total Zn uptake in the first forage harvest only. Significantly lower total Zn uptake values were recorded for crown-root systems as a result of liming.

Phorphorus did not significantly affect Zn composition of hairy indigo forage but increased total Zn uptake in the crown-root systems over control. Since root yields were similar, a P-Zn relationship may have immobilized Zn in the crown-root system.

Phosphorus concentration values of hairy indigo varied from 825 to 4,700 ppm for forage and 775 to 2,275 ppm for crown-root systems. Con-centrations for the three forage harvests and crown-root harvest aver-

aged 2,930, 2,560, 2,820, and 1,290 ppm P, respectively. Total P up-
take averaged 8.69, 10.23, 6.80, and 2.19 mg/pot (equivalent to 4.73,
5.57, 3.70, and 1.19 kg P/ha) for the three forage harvests and crown-
root systems, respectively. Extractable P ranged from 8.1 to 52.9 ppm.

Phosphorus significantly increased extractable P and P composition
of hairy indigo forage and crown-root systems. Although liming decreased
extractable P significantly both P concentration and total uptake values
in hairy indigo forage were significantly increased. Beneficial effects
of lime on forage yields and on various soil fertility factors out-
weighed the negative effect on extractable P. Lime however had no
effect on P composition of crown-root systems.

Zinc did not significantly affect P nutrition of hairy indigo. In
general forage P compositions of hairy indigo were over two-fold higher
than those values recorded for jaraguagrass forage. Crown-root P con-
centrations of hairy indigo were about 60% higher than jaraguagrass
crown-root systems but P uptake values were 35% lower. This was es-
sentially due to large yield differences between the crown-root systems
of the legume and grass.

Calcium concentration of hairy indigo varied from 0.70 to 2.53%
for forages and 0.16 to 0.56% for crown-root systems, respectively.
Average concentration values for the three forage harvests and crown-
root harvest were 2.00, 1.76, 1.71, and 0.33% Ca, respectively. Total
Ca uptake averaged 58.66, 72.20, 42.81, and 5.57 mg/pot (equivalent to
31.91, 39.28, 23.29, and 3.03 kg Ca/ha) for the three forage harvests
and crown-root harvest, respectively. Extractable Ca ranged from
3,150 and 5,475 ppm.

Lime significantly increased extractable Ca and Ca composition of

hairy indigo forage. Crown-root systems did not respond to lime amend-
ment. Phosphorus fertilizer also significantly increased extractable
Ca and Ca concentration in the crown-root systems. Total forage Zn
uptake by hairy indigo exceeded corresponding values of jaraguagrass
forage by 50 - 60% for the first two harvests. However, Zn concentra-
tion and total uptake values for indigo crown-root systems were 60%
and 10% lower, respectively, than found for jaraguagrass crown-root
systems.

Nitrogen concentrations of composite hairy indigo forage samples
ranged from 2.18 to 2.81% N (13.63 to 17.56% crude protein). These
high values, which were sustained from harvest to harvest, together
with visual observation of nitrogen nodules on hairy indigo roots
clearly indicated active symbiotic N fixation. Values obtained for
jaraguagrass forage did not exceed 1.74% N (10.88% CP) despite high N
fertilizer applications. Total N content of hairy indigo pot soil
averaged 0.36 and 0.37% for control and fertilized (P_0, Zn_2, and Ca_1)
treatments, respectively.

Fertilized (P_2, Zn_2, and Ca_1 treatment) hairy indigo forage sub-
stantially increased oven-dry yields and total Zn, P, and Ca uptake
over control but crown-root systems showed little response to fertilizers.
This was in contrast to jaraguagrass forage and crown-root systems which
were both responsive to applied nutrients. Despite the small crown-root
system, total nutrient uptake by hairy indigo was generally higher than
the jaraguagrass which had a well-developed crown-root system.

Two field experiments were established at Santa Fe, Patino, and
Yaviza to study the effect of Zn uptake by jaraguagrass grown alone
and by jaraguagrass-hairy indigo mixed swards. Each experiment was a
3+1 randomized block design with treatments replicated three times.

Treatments for the jaraguagrass field study were control and three levels of Zn (0, 15, and 30 kg Zn/ha as zinc sulfate) with a compound fertilizer mixture (100 kg N/ha as urea, 100 kg P/ha as triple super-phosphate, and, for the Santa Fe experiment only, 1,000 kg Ca/ha as slaked lime). All plots received a basic dressing of 90 kg K/ha equivalent. Except for N in the compound fertilizer mixture, treatments for the jaraguagrass-hairy indigo mixed sward experiment were the same.

Field studies gave only preliminary indications of Zn concentration and total uptake of jaraguagrass with Zn and other fertilizer amendments. Forage and soil concentrations for Zn, P, Ca, Mg, Fe, Cu, Mn, and Sr were reported and trends were discussed.

Based on results obtained from the jaraguagrass and hairy indigo experiments, the following observations and conclusions appear to be salient:

1. For the three Panamanian soils used in this investigation, Zn applications had no direct effect on increasing forage yields of jaraguagrass and hairy indigo.

2. Applications of N up to 50 kg N/ha/harvest significantly increased forage and crown-root yields of jaraguagrass by its beneficial effect on root proliferation and plant growth in general.

3. Supply of N was not a limiting factor in the growth of hairy indigo. This was substantiated by the observation of active symbiotic N-fixing root nodules and corresponding high total N concentrations of the forage.

4. Lime applications of 2,000 kg Ca/ha significantly increased yields of jaraguagrass on the strongly acid Santa Fe soil.

This effect was ascribed to the beneficial effects of lime in increasing soil pH and other soil fertility factors. Nitrogen and Ca interactions resulted in a synergistic effect that increased yields of jaraguagrass. Lime significantly increased hairy indigo forage yields but had no measurable effect on the crown-root systems.

5. Applications of P, contrary to expectations, did not significantly affect hairy indigo forage and crown-root yields and significantly influenced jaraguagrass only in the first forage harvest. Apparently adequate P for normal plant growth was supplied by the Santa Fe pot soil.

6. Applications of Zn significantly increased soil extractable Zn in all pot experiments. There was an inverse relationship between extractable Zn and applied lime. This was expected due to the concomitant increase in soil pH which reduced Zn availability.

7. A negative N x P interaction that significantly decreased extractable soil Zn in the jaraguagrass pot experiments implies the formation of compounds of low solubility, such as $ZnNH_4PO_4$.

8. Applications of Zn significantly increased Zn concentrations of jaraguagrass forage and crown-root systems in pot studies and showed a positive trend in the field experiments; however, total Zn uptake by forage was significantly increased only by the Zn_2 (30 kg Zn/ha) treatment. All Zn applications increased total Zn uptake by jaraguagrass crown-root systems.

9. Applications of Zn resulted in no significant increase of Zn concentration in hairy indigo. Evidently, hairy indigo was efficient in utilizing the indigenous soil zinc. A significant

decrease in Zn concentration was obtained in the second harvest
due to a negative Ca x Zn interaction. Except for the second
forage harvest of hairy indigo, applications of Zn did not
increase Zn uptake. Differences in plant yields are critical
since total Zn uptake is a function of Zn concentration and
yield.

10. Zn applied in combination with N significantly increased Zn
concentration and total uptake values of jaraguagrass. This
was a result of plant growth being stimulated by N. Lime
depressed Zn concentration in jaraguagrass but increased
total Zn uptake.

11. Applications of P had no effect on forage Zn uptake or forage
concentrations of jaraguagrass and hairy indigo. However, P
applications significantly increased total Zn uptake by the
crown-root systems. This implied that P immobilized Zn within
or in the vicinity of the crown-root system.

12. Plant concentrations of Zn were relatively high despite low
values of NH_4OAc (pH 7.0) extractable-soil Zn. Evidently,
NH_4OAc (pH 7.0) extractable Zn values underestimated the Zn
supplying-power of the soil.

13. Results seemed to indicate that the Panamanian soils studied
are inherently fertile and, because of the nature of the
colloidal clay fractions, these soils represent a limitless
reservoir capable of retaining soluble fallout cations against
leaching to hydrologic outlets.

14. Application of lime to pastures could reduce total Zn uptake
by forage plants growing on slightly acid or neutral soils.

Liming of strongly acid soils to control Zn uptake may not be entirely effective. On acid Santa Fe soils, jaraguagrass forage yields and hence total Zn uptake were substantially increased by the beneficial effects of liming even though soil-extractable Zn and forage Zn concentrations were depressed.

15. Hairy indigo forage had higher Zn concentration and total Zn uptake values than jaraguagrass which could increase the transfer of fallout Zn to grazing animals. However, hairy indigo forage also contained more Ca which is known to reduce Zn absorption by animals. The implication of this relationship needs further study.

16. Despite a small crown-root system, hairy indigo depleted the soil in the vicinity of the roots more effectively than the well-developed crown-root system of jaraguagrass.

17. Suggested measures for controlling or reducing radionuclide absorption include the following:

    (a) selection of soils;

    (b) addition of competing ions;

    (c) selection of crops; and

    (d) crop management and utilization.

APPENDIX

Table 68. Morphology[1] of soils used for pot studies and field experi-
ments.

Depth (cm)	Description

SANTA FE

Location: About 800 m from Santa Fe 0.1 C.S. Base Camp.
Topography: Complex slopes with 5-10% slope gradients.
Vegetation: A 3-year-old jaraguagrass (<u>H. rufa</u>) pasture
with some <u>Paspalum</u> and <u>Axonopus</u> grass species,
<u>Desmodium</u> sp. and <u>Cyperaceae</u>. Originally of
the Quipo (<u>Cavanillesia platanifolia</u>) forest
type.
Drainage: Imperfectly drained.
Parent Material: Shale.

Profile 1

Depth (cm)	Description
0-7.5	Dark brown (7.5YR 3/2) clay loam; strong fine crumb; friable when moist, sticky, and plastic when wet; abundant fibrous roots; presence of ash and carbonaceous matter from previous burnings; pH 6.1 and 5.6.
7.5-25	Reddish-brown (5YR 5/4) clay; weakly granular to subangular blocky; fine distinct common mottles, red (2.5YR 4/6) and yellow brown (10YR 5/6) colors predominate; smooth and clear boundary; fibrous roots common; pH 4.9 and 4.9.
25-40	Reddish-brown (5YR 4/4) clay; sub-angular blocky; mottles similar to 7.2-25 cm horizon; few roots; pH 4.4 and 4.7.
40-42.5	Similar to 25-40 cm horizon; highly weathered shale becoming prominent; pH 4.2 and 4.6.
42.5-51	Similar to 40-42.5 cm horizon but with a yellow (10YR 7/8) weakly laminated limonitic pan, 4 mm thick, wavy; pH 4.2 and 4.7.
51-110	Very pale brown (10YR 7/4), light yellowish-brown (10YR 7/4), to red (2.5YR 4/6) mottled colors; highly weathered shale with clayey texture; massive to platy, broken with slight pressure; living roots absent; presence of cherty fragments; pH 4.1 and 4.7.
110+	Similar to 51-110 cm horizon; decomposed clayey shale with yellow and gray mottled fragments; pH 4.0 and 4.6.

Table 68. Continued

Depth (cm)	Description

Profile 2

0-6   Very dark gray (7.5YR 3/0), clay loam; strong fine-medium crumb; friable; horizon boundary clear and smooth; random ash deposits within 0-0.5 cm layer; abundant fibrous roots; pH 6.5 and 6.1

6-25   Dark brown (7.5YR 4/2 - 4/4) clay; fine granular to weak sub-angular blocky; friable; distinct common red mottles with limonitic stainings; few roots; pH 4.7 and 4.9.

25-60   Reddish-brown (5YR 5/3) clay; massive to platy; highly weathered shale with gray to grayish-brown mottles; easily broken by hand; roots absent; pH 4.5 to 4.6.

60-90   Similar to 25-60 cm horizon with few limonitic concretions which crumbles easily with slight pressure; pH 4.5 and 4.6.

90-120   Similar to 60-90 cm horizon with red and yellow brown mottles and chert fragments; pH 4.5 and 4.6.

120-150   Similar to 90-120 cm horizon; highly weathered laminated shale with light gray (5YR 7/1) matrix; pH 4.2 and 4.7.

Profile 3

0-6   Dark brown (7.5YR 4/2) clay loam; fine-medium crumb; friable; horizon boundary distinct and smooth; ash deposits present; abundant fibrous roots; pH 5.5 and 5.9.

6-15   Reddish-brown (5YR 4/3 to 5/4) clay; medium granular to sub-angular blocky; few, fine red mottles; few ash deposits; fibrous roots common; pH 5.3 and 5.6.

15-32.5   Reddish-brown (5YR 5/4) clay; weakly sub-angular blocky; common medium red mottles; decomposing roots; pH 4.4 and 4.8.

32.5-60   Pale brown (10YR 6/3) clay; red mottled clay skins around medium angular blocky peds; firm but breaks with hand pressure; pH 4.4 and 4.7.

60-120   Similar to 32.5-60 cm horizon with highly weathered shale; lamination indistinct; pH 4.2 and 4.6.

120-150   Similar to 60-120 cm horizon; weathered shale with more distinct lamination; pH 4.0 and 4.3.

Table 68. Continued

Depth (cm)	Description
150-180	Similar to 120-150 cm; clayey weathered shale distinct lamination; crumbled with difficulty; pH 4.0 and 4.4.

Profile 4

0-5	Very dark brown (10YR 3/3) clay; strong fine crumb; friable; fine faint iron mottles along root channels; ash deposits; abundant fibrous roots; pH 5.5 and 5.5.
5-20	Reddish-brown (5YR 4/3) clay; sub-angular blocky; friable; medium distinct red mottles; evidence of earthworm activity; few roots; pH 5.0 and 4.7.
20-32.5	Dark reddish-brown (5YR 3/3) clay; weakly sub-angular blocky; common fine red mottles; roots absent; pH 4.5 and 4.5.
32.5-60	Similar to 20-32.5 horizon; highly weathered clayey shale with fine red and yellow mottles; weak lamination; pH 4.5 and 4.5.
60-90	Similar to 32.5-60 cm horizon; fine red mottles prominent; shale lamination clear; pH 4.5 and 4.4.
90+	Similar to 60-90 cm horizon; weathered shale; pH 4.4 and 4.5.

PATINO

Location: Approximately 500 m SE of Hammac-Banz ranch house.
Topography: Gently rolling with simple 2-5% slopes.
Vegetation: A 3-year-old jaraguagrass pasture with some Paspalum, Brachiaria, and Desmodium species present as weeds.
Drainage: Imperfect drainage.
Parent Material: Basic igneous rocks.

Profile 1

0-12.5	Dark brown (7.5YR 3/2) clay; strong, fine crumb; friable; abundant fibrous roots; earthworm activity evident; pH 7.5 and 7.0.
12.5-43	Reddish-yellow (5YR 6/8) clay; strong fine crumb; friable; fine distinct common red and yellow mottlings evident; presence of few black concretions; roots plentiful; pH 6.5 and 6.7.

Table 68. Continued

Depth (cm)	Description
43-71	Yellowish-red (5YR 5/6) to dark reddish-brown (5YR 3/4) clay; fine crumb to weakly sub-angular blocky; friable; red and yellow mottles common; few roots; igneous rock fragments; pH 5.9 and 5.6.
71+	Similar to 43-71 cm horizon with increasing abundance of igneous rock fragments and absence of fibrous roots; water-table at about 84 cm depth; pH 5.0 and 5.3.

Profile 2

0-15	Dark brown (7.5YR 3/2) clay; fine, strong crumb; friable; abundant fibrous roots; pH 6.5 and 6.8.
15-45	Reddish-yellow (5YR 6/8) clay; fine, strong crumb; friable roots plentiful; presence of black concretions and few crystalline rock fragments; pH 6.2 and 6.5.
45-75	Yellowish-red (5YR 5/6) to dark reddish-brown (5YR 3/4) clay; fine crumb to weakly sub-angular blocky; friable; red and yellow mottles common; few roots; igneous rock fragments; pH 5.9 and 5.6.
75+	Similar to 43-71 cm horizon with increasing abundance of igneous rock fragments and absence of fibrous roots; water-table at about 84 cm depth; pH 5.0 and 5.3.

YAVIZA

Location: About 1.5 km up Rio Chico from Yaviza.
Topography: Flat alluvial terrace.
Vegetation: A 2-year-old jaraguagrass pasture previously planted in corn (Zea mays) with Panicum, Paspalum, Desmodium, Palmaceae, and Heliconia species present. Natural vegetation is of the Quipo forest type.
Drainage: Imperfectly drained.
Parent Material: Alluvial deposits.

Profile 1

0-15	Dark grayish-brown (10YR 4/2) to dark brown (10YR 4/3) silty clay loam to silty clay; fine granular; friable; abundant fibrous roots; ash present 0-5 mm layer; earthworm activity observed; pH 7.0 and 6.8.

Table 68. Continued

Depth (cm)	Description
15-25	Very dark grayish-brown (10YR 3/2) clay to silty clay; fine crumb to granular; very friable; fine distinct yellowish-brown (10YR 5/4) mottles; ash deposits present; may be an argillic horizon; pH 6.9 and 6.6.
25-60	Dark yellowish-brown (10YR 4/4) to yellowish-brown (10YR 5/4), with depth, clay to silty clay; fine crumb to sub-angular blocky; common, medium, distinct yellowish-brown mottles; few living roots; evidence of water-table about 33 cm from surface; pH 6.8 and 6.8.
60-90	Similar to 25-60 cm horizon but becoming grayish-brown (10YR 5/2); evidence of gleying; pH 6.8 and 6.8.
90-120	Similar to 60-90 cm horizon; mottles no longer prominent; decaying roots present; pH 6.8 and 6.8.

Profile 2

Depth (cm)	Description
0-12	Very dark gray-brown (7.5YR 3/2) silty clay loam to silty clay; fine granular; friable; abundant fibrous roots; ash present 0-5 mm layer; pH 6.8 and 6.6.
12-20	Very dark grayish-brown (10YR 3/2) clay to silty clay; fine crumb to granular; very friable; fine distinct yellowish-brown (10YR 5/4) mottles; ash deposits present; may be an argillic horizon; pH 6.5 and 6.5.
20-52	Dark yellowish-brown (10YR 4/4) to yellowish-brown (10YR 5/4), with depth, clay to silty clay; fine crumb to sub-angular blocky; common, medium, distinct yellowish-brown mottles; few roots; evidence of water-table about 30 cm from surface; pH 6.5 and 6.6.
52-85	Similar to 20-52 cm horizon but becoming grayish-brown (10YR 5/2); evidence of gleying; pH 6.2 and 6.5.
85+	Similar to 52-85 cm horizon; mottles no longer prominent; decaying roots present; pH 6.0 and 6.3.

[1]Symbols express Munsell color notations of moist soils. Values for pH are given in order of color metric determination in the field (Truog kit) and glass electrode on a 1:2 soil:water suspension in the laboratory.

Table 69. Extract analyses[1] and pH of soils used for pot studies and field experiments.

Location and profile number	Depth	pH		Extractable nutrients (ppm)								
		Truog	H₂O	K	P	Ca	Zn	Mg	Fe	Cu	Mn	Sr
Santa Fe Profile 1	0-7.5	6.1	5.6	535	0.7	4,500	2.4	1,950	2.0	0.3	7.0	1.5
	7.5-25	4.9	4.9	320	0.4	1,200	5.6	1,050	1.6	0.2	2.8	1.5
	25-40	4.4	4.7	383	0.4	200	2.7	740	2.0	0.8	1.0	1.0
	40-42.5	4.2	4.6	209	0.4	200	1.5	600	2.0	0.1	0.7	79.0
	42.5-50	4.2	4.7	163	0.4	25	2.5	440	6.7	0.6	N.A.	13.0
	50-110	4.1	4.7	N.A.	0.7	25	3.7	680	1.6	1.8	N.A.	2.0
	110+	4.0	4.6	230	15.4	66	2.3	672	0.4	0.6	8.1	88.8
Profile 2	0-6	6.5	6.1	1,280	14.0	5,200	2.4	1,920	2.2	1.9	2.5	0.9
	6-25	4.7	4.9	490	2.8	196	1.9	1,010	0.7	1.5	2.9	6.2
	25-60	4.5	4.6	190	1.4	28	1.4	735	0.2	1.7	1.0	3.8
	60-90	4.5	4.6	190	0.7	12	2.5	544	0.2	2.4	0.8	2.5
	90-120	4.5	4.6	230	0.7	10	2.3	605	0.5	3.4	N.A.	3.3
	120-150	4.2	4.7	250	1.4	14	3.0	624	0.7	0.7	1.7	2.2
Profile 3	0-6	5.5	5.9	490	16.1	7,400	1.8	1,280	0.3	1.8	31.8	141.5
	6-15	5.5	5.5	160	66.5	4,900	1.7	1,290	1.4	7.9	16.0	134.0
	15-32.5	4.4	4.8	190	7.0	3,300	2.0	1,250	2.5	2.1	0.7	38.4
	32.5-60	4.4	4.7	240	2.1	356	2.7	432	2.3	4.2	4.3	6.8
	60-120	4.2	4.6	230	2.8	25	3.8	305	3.3	5.5	0.7	4.8
	120-150	4.0	4.3	250	1.4	28	6.7	292	3.3	3.4	1.4	2.7
	150-180	4.0	4.4	310	2.1	19	4.6	311	12.9	5.7	0.5	2.6
Profile 4	0-5	5.5	5.5	810	2.8	4,200	6.5	1,600	3.0	2.2	61.9	113.3
	5-20	5.0	4.7	350	7.0	5,475	2.0	2,190	6.2	0.9	23.2	31.1
	20-32.5	4.5	4.5	310	0.4	481	1.6	744	1.8	6.1	5.7	11.6

Table 69. Continued

Location and profile number	Depth	pH		Extractable nutrients								
		Truog	H₂O	K	P	Ca	Zn	Mg	Fe	Cu	Mn	Sr
	cm							ppm				
Profile 4 Cont'd.	32.5-60	4.5	4.5	290	14.0	31	2.8	544	4.0	4.9	3.3	4.2
	60-30	4.5	4.4	230	8.4	28	1.9	505	12.5	5.6	2.2	2.1
	90+	4.4	4.5	210	4.9	18	4.1	555	2.9	5.7	1.0	3.1
Patino Profile 1	0-12.5	7.5	7.0	550	7.0	3,660	0.8	545	0.1	0.2	36.0	37.0
	12.5-43	6.5	6.7	400	1.4	2,950	1.4	690	1.8	0.3	2.5	31.0
	43-71	5.9	5.6	190	1.4	2,770	0.7	855	0.5	0.5	16.0	34.0
	71+	5.0	5.3	160	1.4	2,850	1.6	890	0.4	0.3	15.0	35.0
Yaviza Profile 1	0-15	7.0	6.8	160	4.2	6,350	1.2	1,200	0.5	0.3	75.0	75.0
	15-25	6.9	6.6	120	2.8	6,260	1.6	1,200	0.8	0.3	36.0	74.0
	25-60	6.8	6.7	130	2.8	5,700	1.4	1,080	1.4	0.5	22.5	77.0
	60-90	6.8	6.8	120	3.5	5,650	1.7	1,230	1.2	0.8	11.0	71.0
	30-120	6.8	6.8	130	2.1	5,350	0.9	1,150	N.D.	0.9	95.0	67.0

[1] pH determined colorimetrically by Truog kit and by glass electrode in a 1:2 soil water suspension.

N.A. - not analyzed
N.D. - not detected
(Fe - less than 0.03 ppm)

Source: Adapted from Gamble et al. (80).

Table 70. Characteristics of surface soils (0-15 cm) used for pot studies and field experiments.

Particle size distribution			Texture	pH[1]	Organic matter	Total N	Extractable nutrients								
Sand	Silt	Clay					K	P	Ca	Zn	Mg	Fe	Cu	Mn	Sr
%	%	%			%	%	ppm								
							Santa Fe								
20	22	58	Clay	5.4	6.8	0.34	690	4.9	3,490	1.5	1,320	0.5	0.5	10	46
							Patino								
11	43	46	Silty clay	7.0	7.2	0.41	280	1.5	3,460	0.9	543	0.4	0.3	39	34
							Yaviza								
18	50	32	Silty clay loam	6.8	6.3	0.35	280	5.1	6,360	1.3	1,070	3.1	0.7	57	74

[1] pH determined by glass electrode on a 1:2 soil:water suspension.

Table 71. Summary of F tests [1] from the analysis of variance of jaraguagrass forage and crown-root systems on yield and elemental composition.

		Yield				Concentration													Total uptake								
		Forage harvest			Crown and roots	Zn				P				Ca				Zn			P			Ca		
						Forage harvest			Crown and roots	Forage harvest			Crown and roots	Forage harvest			Crown and roots	Forage harvest			Forage harvest			Forage harvest		
Source	d.f.	1	2	3		1	2	3		1	2	3		1	2	3		1	2	3	1	2	3	1	2	3
Replication	2	**	**	**	**	**	**	**		***			*	**	**	**		**	**	**	*	**	**	**	**	**
Treatment	53	**	**	**	**	**	**	**		***	***	***		***	**	**		***	**	**	***	**	**	***	**	**
N	2	**			**	**	**	**	*	*	**	**													**	*	**
NxP	4											**															
Ca	1	**	**	**	**	**	**	*		**	*			**	**	**		**	**	**	**	**	**	**	**	**
NxCa	2	**	**	**	**	**	**	*		*			**	**	**	*	**	**	**	**	**	**	**			**
PxCa	2										*						*						*		*		**
NxPxCa	4	**																									**
Zn	2					**	**	**	**	**								**	*	**			*				**
NxZn	4	*																									
PxZn	8																										
NxPxZn	2			*																							
CaxZn	2																										
NxCaxZn	4	*																									
PxCaxZn	4																										
NxPxCaxZn	8																										
Error	106																										

[1] Voids are not significant.

* - Significant at the 5% level.
** - Significant at the 1% level.

Table 72. Summary of F tests[1] from the analysis of variance on soil pH and extractable nutrients from jaraguagrass pot experiment.

Source	d.f.	pH (H_2O)	pH (KCl)	Extractable nutrients Zn	P	Ca
Replication	2	**	**			**
Treatment	53					
N	2		**			
P	2				**	
N x P	4	**		*		
Ca	1	**	**	**	**	**
N x Ca	2					
P x Ca	2					
N x P x Ca	4					
Zn	2			**		
N x Zn	4					
P x Zn	4					
N x P x Zn	8					
Ca x Zn	2					
N x Ca x Zn	4					
P x Ca x Zn	4				*	
N x P x Ca x Zn	8					
Error	106					

[1]Voids are not significant.

* - Significant at the 5% level.

** - Significant at the 1% level.

Table 73. Multiple regression model for jaraguagrass pot experiment.

Model: $\hat{y} = \bar{y} + b_1\,x_1 + b_2\,x_2 + b_3\,x_3 + b_4\,x_4 + b_5\,x_5 + b_6\,x_6 + b_7\,x_7$
$+ b_8\,x_3\,x_1 + b_9\,x_3\,x_2 + b_{10}\,x_4\,x_1 + b_{11}\,x_3\,x_5 + b_{12}\,x_3\,x_6$
$+ b_{13}\,x_4\,x_5 + b_{14}\,x_4\,x_6 + b_{15}\,x_3\,x_7 + b_{16}\,x_4\,x_7 + b_{17}\,x_5\,x_7$
$+ b_{18}\,x_6\,x_7 + \xi,$

where:

$\hat{y}$ = estimated response value (such as yield, elemental composi-
tion of jaraguagrass, extractable soil nutrients or soil pH);

$\bar{y}$ = constant or general mean value given in Table 74 for the
specific response;

$x_1 = \dfrac{kg\ Zn/ha}{15} - 1$ = Zn linear variable (Zn_L);

$x_2 = \left| \dfrac{kg\ Zn/ha}{15} + 1 \right|^2 - 12 \left| \dfrac{kg\ Zn/ha}{15} + 1 \right| + 10$

= Zn quadratic variable (Zn_Q);

$x_3 = \dfrac{kg\ N/ha}{50} - 1$ = N linear variable (N_L);

$x_4 = 3 \left| \dfrac{kg\ N/ha}{50} + 1 \right|^2 - 12 \left| \dfrac{kg\ N/ha}{50} + 1 \right| + 10$

= N quadratic variable (N_Q);

$x_5 = \dfrac{kg\ P/ha}{50} - 1$ = P linear variable (P_L);

$x_6 = 3 \left| \dfrac{kg\ P/ha}{50} + 1 \right|^2 - 12 \left| \dfrac{kg\ P/ha}{50} + 1 \right| + 10$

= P quadratic variable (P_Q);

$x_7 = \dfrac{kg\ Ca/ha}{1,000} - 1$ = Ca linear variable (Ca_L);

b_1 to $_{18}$ = regression coefficients given in Table 74 for each specific
independent variable or interaction;

and, ξ = experimental error or random element of the variable.

Table 74. Coefficients for multiple regression model of jaraguagrass pot experiment.[1]

Response	$\hat{y}^2$	Zn		N		P		Ca	NxZn			NxP				NxCa		PxCa	
		x_1 b_1	x_2 b_2	x_3 b_3	x_4 b_4	x_5 b_5	x_6 b_6	x_7 b_7	x_3x_1 b_8	x_3x_2 b_9	x_4x_1 b_{10}	x_3x_5 b_{11}	x_3x_6 b_{12}	x_4x_5 b_{13}	x_4x_6 b_{14}	x_3x_7 b_{15}	x_4x_7 b_{16}	x_5x_7 b_{17}	x_6x_7 b_{18}
Yield (g/pot)																			
Forage 1	2.43	0.054		0.481	-0.087	0.092	-0.054	0.339	0.014		-0.049					0.232			
Forage 2	2.58	0.026	0.065	0.508	-0.173			0.772	-0.099	-0.139	-0.110					0.660			
Forage 3	2.62			1.311	-0.440	0.151		0.957								1.359		-0.346	
Crown & roots	9.44	0.383		1.551	-0.905			1.845	-0.074		0.314	0.199							
Zn concentration (ppm)																			
Forage 1	22	2.07		2.10				-0.38	1.85							-1.07			
Forage 2	40	3.44		5.54	-0.88			-0.29	2.35							-2.44			
Forage 3	43	4.21		5.80				-2.88											
Crown & roots	157	38.44						-16.84	20.39										
Zn total uptake (mg/pot)																			
Forage 1	55	6		16				6								13			
Forage 2	101	9		32	-9			26								24			
Forage 3	137	15		65	-19			33	0.6		-6								
P concentration (ppm)																			
Forage 1	986			-126	56	63		62				-62							
Forage 2	1,473			-448	141	239		159					83						
Forage 3	1,285			-457	121	170		72				-15	83	16					
Crown & roots	533					89	24	21							40				

Table 74. Continued

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Response	$\bar{y}^2$	Zn x_1 b_1	Zn x_2 b_2	N x_3 b_3	N x_4 b_4	P x_5 b_5	P x_6 b_6	Ca x_7 b_7	NxZn x_3x_1 b_8	NxZn x_3x_2 b_9	x_4x_1 b_{10}	x_3x_5 b_{11}	NxP x_3x_6 b_{12}	NxP x_4x_5 b_{13}	NxP x_4x_6 b_{14}	NxCa x_3x_7 b_{15}	NxCa x_4x_7 b_{16}	PxCa x_5x_7 b_{17}	PxCa x_6x_7 b_{18}
P total uptake (mg/pot)																			
Forage 1	2.37					0.22		0.50											
Forage 2	3.61			0.21		0.54		1.14											
Forage 3	3.62	0.26	0.28	0.62	-0.36	0.69	-0.15	1.23	0.05	-0.18	-0.19	0.29	-0.20	0.004	0.10	0.54			0.27
Ca concentration (ppm)																			
Forage 1	4,952			-672	181	-85		275								146	128	146	
Forage 2	5,388			-840	213	50		395								-250			
Forage 3	5,403			-703	302			330								-256			190
Crown & roots	3,300	186						241											
Ca total uptake (mg/pot)																			
Forage 1	11.80	0.09	0.48	0.89	-0.49	0.30		2.39	-0.59	0.55						-0.04	-0.23	0.44	
Forage 2	13.62	0.72	0.52	0.72	-1.68	1.00		4.87								2.94			
Forage 3	16.30	0.65		5.36				5.70											

Table 74. Continued

Response	$\bar{y}^2$	Zn x_1 b_1	x_2 b_2	N x_3 b_3	x_4 b_4	P x_5 b_5	x_6 b_6	Ca x_7 b_7	NxZn x_3x_1 b_8	x_3x_2 b_9	x_4x_1 b_{10}	NxP x_3x_5 b_{11}	x_3x_6 b_{12}	x_4x_5 b_{13}	x_4x_6 b_{14}	NxCa x_3x_7 b_{15}	x_4x_7 b_{16}	PxCa x_5x_7 b_{17}	x_6x_7 b_{18}
Soil Analyses																			
Zn (ppm)	0.76	0.166		-0.007		-0.018	-0.017	-0.140				-0.013	0.052						
P (ppm)	25.9			1.71	-0.54	9.56	-0.21	-4.70				-0.51	0.65	-1.57					
Ca (ppm)	4,265			32		57		945				69							
pH (H2O)	5.60			0.008	-0.002	0.015	-0.001	0.370				0.004	-0.007	0.023					
pH (KCl)	4.57			-0.029	0.011			0.417											

¹Refer to Table 73 for multiple regression model.

$\bar{y}^2$ = constant or general mean value.

Table 75. Effect of applied nutrients on other elemental concentrations in jaraguagrass forage.

Treatment[1]	Mg Harvest 1	Mg Harvest 2	Mg Harvest 3	Fe Harvest 1	Fe Harvest 2	Fe Harvest 2	Cu Harvest 1	Cu Harvest 2	Cu Harvest 2	Mn Harvest 1	Mn Harvest 2	Mn Harvest 3	Sr Harvest 1	Sr Harvest 2	Sr Harvest 3
									ppm						
Zn_0	1,870	1,960	2,050	88	79	70	17	13	15	48	36	40	34	38	40
Zn_1	1,850	2,000	1,990	86	80	69	15	13	13	36	34	40	37	38	40
Zn_2	1,840	1,990	2,000	82	80	79	16	12	15	37	30	41	33	37	40
N_0	1,830	1,950	2,310	69	65	69	14	10	12	43	32	40	41	44	44
N_1	1,830	1,930	1,820	86	88	69	17	14	14	38	37	40	32	36	39
N_2	1,910	2,060	1,990	101	87	80	18	14	17	41	31	41	29	34	39
P_0	1,870	1,980	1,950	80	79	71	17	13	14	47	33	38	35	39	40
P_1	1,890	1,990	2,050	86	83	72	17	13	13	41	82	41	35	37	41
P_2	1,800	1,970	2,030	90	78	75	15	12	16	33	35	43	32	37	40
Ca_0	1,870	2,030	1,950	80	76	71	17	12	14	46	46	38	35	38	40
Ca_1	1,890	1,930	2,050	86	83	72	17	13	13	41	21	41	35	38	41
Range:															
Minimum	1,450	1,450	1,750	29	21	17	1	5	0	1	5	8	16	20	25
Maximum	4,300	2,920	5,700	210	368	240	40	40	35	186	170	195	63	70	60

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, N_0, N_1, and N_2 to 0, 50, and 100 kg N/ha; P_0, P_1, and P_2 to 0, 50, 100 kg P/ha; and Ca_0 and Ca_1 to 0 and 2,000 kg Ca/ha, respectively.

Table 76. Comparison of oven-dry yields and elemental composition between control and fertilized forage and crown-root systems from jaraguagrass pot experiment.

Harvest	Yield	Concentration			Total uptake		
		Zn	P	Ca	Zn	P	Ca
	g/pot	------- ppm -------			ug/pot	--- mg/pot ---	
				Control[1]			
Forage 1	1.52	18	760	5,900	27	1.15	8.97
2	1.65	32	1,410	5,210	53	2.32	8.60
3	1.18	37	1,630	6,250	44	1.92	7.38
Crown and roots	7.03	129	400	2,330	907	2.81	16.38
				Fertilized[2]			
Forage 1	3.58	27	950	4,850	97	3.40	17.37
2	3.39	41	1,730	5,080	139	5.87	17.22
3	5.86	46	1,200	5,370	270	7.03	31.49
Crown and roots	12.55	208	658	3,170	2,610	8.26	39.75

[1]Control treatment refers to jaraguagrass which received a basic equivalent application of 90 kg K/ha only.

[2]Fertilized treatment refers to jaraguagrass which received the equivalent of 90 kg K/ha, 100 kg N/ha, 100 kg P/ha, 30 kg Zn/ha and 2,000 kg Ca/ha.

Table 77. Comparison of soil pH and extractable nutrients betweeen
untreated, control, and fertilized soils from jaraguagrass
pot experiment.

Soil treatment [1]	pH		Extractable nutrients		
	(H_2O)	(KCl)	Zn	P	Ca
			----------- ppm -----------		
Untreated	5.40	4.33	2.5	13.7	4,700
Control	5.33	4.23	0.9	13.3	3,342
Fertilized	6.30	5.03	0.6	13.4	5,475

[1] Soil treatments were: untreated pot soil prior to experiment;
control soil after cropping, with a basic equivalent application
of 90 kg K/ha; and fertilized soil after cropping, with equivalent
applications of 90 kg K/ha, 100 kg N/ha, 100 kg P/ha, 30 kg Zn/ha,
and 2,000 kg Ca/ha.

Table 78. Nutrient recovery from jaraguagrass pot experiment.

Nutrient compartment	Treatment									
	Zn_1		Zn_2		P_1		P_2		Ca_1	
	ug/pot	%	ug/pot	%	mg/pot	%	mg/pot	%	mg/pot	%
Total applied	24,016	100.00	48,033	100.00	92.00	100.00	184.00	100.00	3,680	100.00
Total crown-root uptake	490	2.04	1,018	2.12	2.40	2.61	2.78	1.51	24	0.65
Total forage uptake	156	0.65	206	0.43	4.79	5.21	5.40	2.94	30	0.82
Soil	23,370	97.31	46,809	97.45	84.81	92.18	175.82	95.55	3,626	98.53

[1] Treatments Zn_1, and Zn_2, were equivalent to 15 and 30 kg Zn/ha; P_1 and P_2 to 50 and 100 kg P/ha; and Ca_1 to 2,000 kg Ca/ha, respectively.

Table 79. Summary of F tests[1] from the analysis of variance of hairy indigo forage and crown-root systems on yield and elemental composition.

Source of variance	d.f.	Yield				Concentration												Total uptake								
						Zn				P				Ca				Zn			P			Ca		
		Forage harvest			Crown and root	Forage harvest			Crown and root	Forage harvest			Crown and root	Forage harvest			Crown and root	Forage harvest			Forage harvest			Forage harvest		
		1	2	3		1	2	3		1	2	3		1	2	3		1	2	3	1	2	3	1	2	3
Replication	2																									
Treatments	17																									
P	1		**	**			**	**			**	**		**	**	**						**	**			
Ca	1												*	**	**	**		*				**	**	**	***	***	*
P.Ca	2																***					*					
Zn	2						**																				
P×Zn	4																										
Ca×Zn	2				*				*																		
P×Ca×Zn	4																										
Error	34																									

[1] Voids are not significant.

* - significant at the 5% level.
** - significant at the 1% level.

Table 80. Summary of F tests[1] from the analysis of variance on soil pH and extractable nutrients from hairy indigo pot experiment.

Source of variance	d.f.	pH (H_2)	pH (KCl)	Extractable nutrients Zn	P	Ca
Replication	2		*		**	**
Treatment	17					
P	2		*		**	**
Ca	1	**	**	**	**	**
P x Ca	2					
Zn	2					
P x Zn	4					
Ca x Zn	2			*		
P x Ca x Zn	4					
Error	34					

[1]Voids are not significant.

* - Significant at the 5% level.
** - Significant at the 1% level.

Table 81. Multiple regression model for hairy indigo pot experiment.

Model: $\hat{Y} = \bar{Y} + d_1 z_1 + d_2 z_2 + d_3 z_3 + d_4 z_4 + d_5 z_5 + d_6 z_3 z_5 + d_7 z_1 z_5$

$\qquad + d_8 z_2 z_5 + \xi,$

where,

$\hat{Y}$ = estimated response value (such as yield, elemental composition of hairy indigo, extractable soil nutrients, or soil pH);

$\bar{Y}$ = constant or general mean value given in Table 82 for the specific response;

$z_1 = \dfrac{\text{kg Zn/ha}}{15} - 1 = $ Zn linear variable (Zn_L);

$z_2 = 3 \left| \dfrac{\text{kg Zn/ha}}{15} + 1 \right|^2 - 12 \left| \dfrac{\text{kg Zn/ha}}{15} + 1 \right| + 10$

$\qquad = $ Zn quadratic variable (Zn_Q);

$z_3 = \dfrac{\text{kg P/ha}}{50} - 1 = $ P linear variable (P_L);

$z_4 = 3 \left| \dfrac{\text{kg P/ha}}{50} + 1 \right|^2 - 12 \left| \dfrac{\text{kg P/ha}}{50} + 1 \right| + 10$

$\qquad = $ P quadratic variable (P_Q);

$z_5 = \dfrac{\text{kg Ca/ha}}{1,000} - 1 = $ Ca linear variable (Ca_L);

d_1 to 8 = regression coefficients given in Table 82 specific independent variable or interaction;

and ξ = experimental error or random element of the variable.

Table 82. Coefficients[1] for multiple regression model of hairy indigo pot experiment.

Response	$\bar{Y}^2$	Zn $z_1 d_1$	Zn $z_2 d_2$	P $z_3 d_3$	P $z_4 d_4$	Ca $z_5 d_5$	P x Ca $z_3 z_5 d_6$	Zn x Ca $z_1 z_5 d_7$	Zn x Ca $z_2 z_5 d_8$
Yield (g/pot)									
Forage 1	2.90					0.186			
Forage 2	4.03					0.537			
Forage 3	2.49					0.303			
Crown & roots	1.70	-0.020	-0.038			0.174		0.058	0.083
Zn concentration (ppm)									
Forage 1	36								
Forage 2	41	0.860				-3.28		-1.97	
Forage 3	43	0.045				-1.82		-1.50	
Crown & roots	100					-27.07			
Zn total uptake (ug/pot)									
Forage 1	106					10.5			
Forage 2	163								
Forage 3	104								
P concentration (ppm)									
Forage 1	2,929			629	-163	436			
Forage 2	2,562			621	289	307			
Forage 3	2,819			581					
Crown & roots	1,289								

Table 82. Continued

Response	$\bar{y}^2$	Zn $z_1 d_1$	Zn $z_2 d_2$	P $z_3 d_3$	P $z_4 d_4$	Ca $z_5 d_5$	P x Ca $z_3 z_5 d_5$	Zn x Ca $z_1 z_5 d_7$	Zn x Ca $z_2 z_5 d_8$
P total uptake (mg/pot)									
Forage 1	8.69			2.21	0.54	1.79			
Forage 2	10.23			2.53	-	2.64	1.10		
Forage 3	6.80				0.33	1.53			
Ca concentration (%)									
Forage 1	2.00					0.223			
Forage 2	1.76					0.157			
Forage 3	1.71					0.127			
Crown & roots	3.25								
Ca total uptake (mg/pot)									
Forage 1	58.66					10.11			
Forage 2	72.20					16.03			
Forage 3	42.81					8.68			

Table 82. Continued

Response	$\bar{Y}$[2]	Zn $\dfrac{z_1}{d_1}$	Zn $\dfrac{z_2}{d_2}$	P $\dfrac{z_3}{d_3}$	P $\dfrac{z_4}{d_4}$	Ca $\dfrac{z_5}{d_5}$	P x Ca $\dfrac{z_3 z_5}{d_6}$	Zn x Ca $\dfrac{z_1 z_5}{d_7}$	Zn x Ca $\dfrac{z_2 z_5}{d_8}$
Soil analyses									
Zn (ppm)	0.73	0.124				-0.176			
P (ppm)	26.1			10.08	0.96	-2.72			
Ca (ppm)	4,345			66		992		-0.194	
pH (H_2O)	5.53			0.194		0.393			
pH (KCl)	4.50					0.428			

[1] Refer to Table 81 for multiple regression model.

[2] $\bar{y}$ = constant or general mean value for the specific response.

Table 83. Effect of applied Zn, P, and Ca on other elemental concentrations in hairy indigo forage.

Treatment[1]	Mg Harvest 1	2	3	Fe Harvest 1	2	3	Cu Harvest 1	2	3	Mn Harvest 1	2	3	Sr Harvest 1	2	3
							ppm								
Zn_0	3,930	3,440	3,770	214	93	74	10	9	11	23	12	17	157	146	149
Zn_1	3,730	3,370	3,620	153	59	72	11	9	10	33	8	12	145	143	150
Zn_2	3,670	3,390	3,660	169	68	83	13	10	10	30	13	13	152	155	152
P_0	3,670	3,250	3,560	137	68	65	11	9	9	28	10	11	151	146	155
P_1	3,850	3,470	3,690	167	67	88	12	9	9	31	12	12	159	156	153
P_2	3,810	3,490	3,800	232	84	75	12	8	12	27	10	17	144	141	142
Ca_0	3,690	3,510	3,950	154	66	77	11	9	9	40	14	16	166	156	170
Ca_1	3,860	3,300	3,420	203	80	75	12	9	11	17	7	12	137	139	130
Range:															
Minimum	2,850	2,850	3,150	55	40	28	10	7	5	10	6	5	20	115	115
Maximum	4,400	4,400	4,450	1,077	190	200	20	29	15	72	48	40	225	200	225

[1]Treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha; P_0, P_1, and P_2 to 0, 50, and 100 kg P/ha, and Ca_0 and Ca_1 to 0, and 2,000 kg/ha, respectively.

Table 84. Comparison of oven-dry yields and elemental composition
between control and fertilized forage and crown-root
systems from hairy indigo pot experiment.

Harvest	Yield	Concentration			Total uptake		
		Zn	P	Ca	Zn	P	Ca
	g/pot	--- ppm ---		%	ug/pot	--- mg/pot ----	
				Control[1]			
Forage 1	2.50	34	1,690	1.86	85	4.23	46.50
2	3.04	42	1,540	1.57	128	4.69	47.68
3	1.89	43	1,910	1.55	81	3.61	29.36
Crown and roots	1.80	89	1,030	0.29	160	1.85	5.25
				Fertilized[2]			
Forage 1	3.44	42	3,760	2.38	145	12.93	81.76
2	5.20	37	3,180	2.00	192	16.55	104.00
3	3.10	41	3,580	1.81	127	11.10	56.11
Crown and roots	1.94	78	1,180	0.31	151	2.28	6.43

[1]Control treatment refers to hairy indigo which received a basic
equivalent application of 90 kg K/ha only.

[2]Fertilized treatment refers to hairy indigo which received the
equivalent of 90 kg K/ha, 100 kg P/ha, 30 kg Zn/ha, and 2,000 kg
Ca/ha.

Table 85. Comparison of soil pH and extractable nutrients between untreated, control, and fertilized soils from hairy indigo pot experiment.

Soil treatment [1]	pH		Extractable nutrients		
	(H$_2$O)	(KCl)	Zn	P	Ca
			----------- ppm ----------		
Untreated	5.40	4.33	2.5	13.7	4,700
Control	5.10	4.10	0.6	21.4	3,270
Fertilized	5.90	5.00	0.5	32.8	5,333

[1] Soil treatments were: untreated pot soil prior to experiment; control soil after cropping with a basic equivalent application of 90 kg K/ha; and fertilized soil after cropping, with equivalent applications of 90 kg K/ha, 100 kg P/ha, 30 kg Zn/ha, and 2,000 kg Ca/ha.

Table 86. Nutrient recovery from hairy indigo pot experiment.

Nutrient compartment	Treatment[1]									
	Zn_1		Zn_2		P_1		P_2		Ca_1	
	ug/pot	%	ug/pot	%	mg/pot	%	mg/pot	%	mg/pot	%
Total applied	24,016	100.00	48,033	100.00	92.00	100.00	184.00	100.00	3,680	100.00
Total crown-root uptake	29	0.12	7	0.02	0.35	0.38	0.72	0.39	--	0.00
Total forage uptake	86	0.36	93	0.19	15.00	16.30	18.00	9.78	85	2.31
Soil	23,901	99.52	47,933	99.79	76.65	83.32	165.28	89.83	3,595	97.69

[1]Treatments Zn_1 and Zn_2 were equivalent to 15 and 30 kg Zn/ha; P_1 and P_2 to 50 and 100 kg P/ha; and Ca_1 to 2,000 kg Ca/ha, respectively.

Table 87. Summary of F[1] tests from the analysis of variance on oven-dry yields and elemental composition of jaraguagrass forage from field experiments.

Location and harvest	Yield	Concentration			Total uptake								Concentration				
		Zn	P	Ca	Zn	P	Ca	Mg	Fe	Cu	Mn	Sr	Mg	Fe	Cu	Mn	Sr
Jaraguagrass experiment																	
Santa Fe																	
1st harvest		*															
2nd harvest																	
Patino																	
1st harvest			*		*											*	
Yaviza																	
1st harvest		**			**												
Mixed sward experiment																	
Santa Fe																	
1st harvest		**															
2nd harvest																	
Patino																	
1st harvest	*		*				*	*							*		
Yaviza																	
1st harvest		*	*														
2nd harvest		**	*					*									

[1]Voids are not significant

* - Significant at the 5% level.
** - Significant at the 1% level.

Table 88. Effect of Zn and fertilizer amendment on Mg, Fe, Cu, Mn, and Sr concentrations of jaraguagrass forage from field experiments.

Treatments[1]	Patino	Yaviza	Santa Fe	
			Harvest	
	1	1	1	2
			ppm	
			Mg	
Control	1,460 a[2]	1,680 a	2,330 a	2,390 a
Zn_0	1,620 a	1,580 a	2,130 a	2,260 a
Zn_1	1,550 a	1,530 a	2,200 a	2,380 a
Zn_2	1,560 a	1,850 a	2,140 a	2,230 a
			Fe	
Control	70 a	83 b	253 a	58 a
Zn_0	90 a	69 a	70 a	68 a
Zn_1	94 a	102 b	95 a	56 a
Zn_2	59 a	155 b	98 a	119 a
			Cu	
Control	12 a	13 a	23 a	7 a
Zn_0	22 a	28 a	18 a	9 a
Zn_1	25 a	20 a	22 a	5 a
Zn_2	24 a	30 a	18 a	8 a
			Mn	
Control	13 a	27 b	43 a	37 a
Zn_0	13 a	23 b	23 a	17 a
Zn_1	17 b	13 a	20 a	17 a
Zn_2	23 b	23 b	13 a	17 a

Table 88. Continued

Treatments[1]	Patino	Yaviza	Santa Fe	
			Harvest	
	1	1	1	2
	ppm			
	Sr			
Control	33 a	23 a	37 a	23 a
Zn_0	23 a	23 a	40 a	27 a
Zn_1	23 a	30 a	37 a	27 a
Zn_2	27 a	53 a	23 a	27 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1, and Zn_2 were equivalent to 0, 15, and 30 kg/ha, respectively, together with an equivalent application of 2,000 kg ca/ha (Santa Fe only), 100 kg N/ha, and 100 kg P/ha.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

Table 89. Effect of Zn and fertilizer amendments on Mg, Fe, Cu, Mn, and Sr concentrations of jaraguagrass forage from the mixed sward field experiments.

Treatment[1]	Patino	Yaviza		Santa Fe	
		Harvest			
	1	1	2	1	2
	ppm				
Mg					
Control	1,400 ab[2]	1,570 a	1,620 a	2,230 a	1,800 a
Zn_0	1,640 b	1,640 a	1,500 a	2,050 a	2,290 a
Zn_1	1,270 a	1,570 a	1,560 a	1,980 a	2,120 a
Zn_2	1,400 ab	1,290 a	1,530 a	1,800 a	2,010 a
Fe					
Control	180 a	150 a	414 a	59 a	60 a
Zn_0	162 a	70 a	503 a	94 a	95 a
Zn_1	155 a	63 a	499 a	89 a	106 a
Zn_2	244 a	40 a	425 a	79 a	75 a
Cu					
Control	17 a	20 a	4 a	18 a	9 a
Zn_0	30 b	18 a	13 a	18 a	9 a
Zn_1	20 a	20 a	9 a	15 a	5 a
Zn_2	17 a	13 a	10 a	16 a	4 a
Mn					
Control	30 a	23 ab	23 a	20 a	10 a
Zn_0	27 a	40 b	27 a	17 a	23 a
Zn_1	27 a	27 ab	23 a	13 a	10 a
Zn_2	23 a	20 a	23 a	27 a	13 a

Table 89. Continued

Treatment[1]	Patino	Yaviza		Santa Fe	
		Harvest			
	1	1	2	1	2
	ppm				
	Sr				
Control	30 a	33 a	30 a	33 a	23 a
Zn_0	27 a	40 a	27 a	27 a	27 a
Zn_1	27 a	30 a	27 a	20 a	27 a
Zn_2	23 a	33 a	30 a	27 a	27 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1 and Zn_2 were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with an equivalent application of 2,000 kg Ca/ha (Santa Fe only) and 100 kg P/ha.

[2]Values followed by the same letter in each column of the specific treatment groups are not significantly different at 0.05 probability level.

Table 90. Effect of Zn and fertilizer amendments on elemental con-
centrations of hairy indigo forage from the mixed sward
field experiment at Yaviza.

Treatment[1]	Concentration							
	Ca	Zn	P	Mg	Fe	Cu	Mn	Sr
	--%--	ppm						
Control	1.775 a[2]	22 a	2,530 a	2,870 a	267 b	7 a	23 a	83 a
Zn_0	1.950 a	22 a	3,550 ab	3,230 a	167 ab	8 a	23 a	77 a
Zn_1	1.908 a	30 a	3,910 b	3,010 a	173 ab	7 a	27 a	80 a
Zn_2	1.658 a	33 a	3,850 b	2,780 a	128 a	5 a	17 a	70 a

[1]Control plots were not fertilized and treatments Zn_0, Zn_1 and Zn_2
were equivalent to 0, 15, and 30 kg Zn/ha, respectively, together with
an equivalent application of 2,000 kg Ca/ha (Santa Fe only), and 100 kg
P/ha.

[2]Values followed by the same letter in each column are not significantly
different at 0.05 probability level.

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BIOGRAPHICAL SKETCH

Michael William Silvey was born in Shanghai, China on January 29, 1941. He attended King George V School in Hong Kong from which he was matriculated in July, 1959. He was awarded the Peace Memorial Scholarship to study agriculture at Wye College, University of London, Kent, England. Prior to reading for his degree, he worked for one year as an Agricultural Apprentice at MacRoberts Estates, Douneside, Aberdeenshire, Scotland. He entered the University of London in October, 1960, and received the degree of Bachelor of Science in Agriculture in August, 1963. Following the award of a United Kingdom Post-graduate Scholarship, he entered the College of Agriculture, University of the West Indies, Trinidad in August, 1963, and received the Diploma in Tropical Agriculture in July, 1964. Upon returning to England, he signed a contract with the Ministry of Overseas Development, United Kingdom Government to work for the Department of Agriculture, Government of British Honduras as Research Agronomist at Central Farm, Cayo, British Honduras. He conducted applied research in major food crops and pastures.

In January, 1967, he was admitted to the Graduate School of the University of Florida and was granted an assistantship from the Center for Tropical Agriculture. From April to September, 1967, he was a member of the University of Florida field team engaged in the Agricultural Ecology Survey of the Darien Province of Panama for the proposed new sea-level canal project. Since September, 1967, he has continued his work towards the degree of Doctor of Philosophy with a major in soils.

The author is married to the former Anne Jeanette Pritchard and they have three children; Sean, Patrick and Amanda. He is a life-member of the Agricola and Swanley Guild and a member of Gamma Sigma Delta, Sigma Xi, Phi Kappa Phi, and Phi Sigma honorary societies, American Society of Agronomy and Soil Science Society of America.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Victor W. Carlisle, Chairman
Associate Professor of Soils

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Gamole
Associate Professor of Environ-
mental Engineering

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William G. Blue
Professor of Soils

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O. Charles Ruelke
Professor of Agronomy

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Clarence B. Ammerman
Professor of Animal Science

This dissertation was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March, 1971

Dean, College of Agriculture

Dean, Graduate School